So Happy Together

Social Behaviour & Song Learning
in Zebra Finches

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Social Behaviour & Song Learning in Zebra Finches

mit deutscher Zusammenfassung

met Nederlandse samenvatting

DISSERTATION

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“Anyone who has never made a mistake has never tried anything new.”
Albert Einstein

“Take risks: if you win, you will be happy; if you lose, you will be wise.”
Anonymous

“To kill an error is as good a service as, and sometimes even better than, the establishing of a new truth or fact.”
Charles Darwin

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Preface

“Here now is Birdsong. Everything that is sweet and melodious. Let us retain this for the preface.”

These are the opening words of a letter, with which Dr. Jac. P. Thijsse handed in the manuscript for a ‘Verkade-Album’ named ‘Birdsong’ in March 1938, which was eventually published in 1965 (Vogelzang. Dr. Jac. P. Thijsse 1938. Published by Koninklijke Verkade Fabrieken N.V. Zaandam 1965). Verkade is a Dutch company that is most famous for its Dutch rusk, biscuits and chocolate. The famous albums started out as a marketing campaign. Pictures were enclosed in packages of cake and tins of Dutch rusk, which could be glued into the albums. Most of the albums had biological topics and contributed to the knowledge of and commitment to nature among the people.

The album cited here is about birdsong and describes how lovely the Dutch endemic species sing. I do not know how Dr. Jac. P. Thijsse would have described the song of the Zebra Finch, but personally, I was not very impressed when I started my PhD-project. However, the more time I spent working on this topic, the more interesting aspects I discovered, and it is fun to study Zebra Finch behaviour.

The main aim of my PhD-project was to get more insight in various aspects of song, song learning and social life of zebra finches. This is all part of a complex system, which could be compared to a puzzle: a clear picture emerges when all pieces are in its place. I am definitely not suggesting that I can complete the picture, but I hope that I can contribute some small pieces with this thesis.

Vorwort

„Hier nun ist der Vogelsang. All was lieblich ist und wohlklingend. Lasst uns dies festhalten für das Vorwort.“
Dies ist der Anfang eines Briefes, mit dem Dr. Jac. P. Thijsse in März 1938 das Manuskript für ein Verkade-Album namens ‘Vogelsang’ einreichte, das letztendlich in 1965 veröffentlicht wurde (Vogelzang. Dr. Jac. P. Thijsse 1938. Published by Koninklijke Verkade Fabrieken N.V. Zaandam 1965). Verkade ist ein Niederländisches Unternehmen, das vor allem durch die Herstellung von Zwieback, Keksen und Schokolade bekannt geworden ist.

Ursprünglich dienten die Verkade-Alben als Werbe-Aktion. In jeder Packung Kuchen und Zwieback befanden sich Bilder, die in die Sammelalben eingeklebt werden konnten. Die meiste Alben beschäftigten sich mit biologischen Themen und förderten so Wissen und Engagement zur Natur unter der Bevölkerung.

Das hier zitierte Album behandelt den Vogelgesang und beschreibt, wie schön die niederländischen einheimische Arten singen. Ich weiss zwar nicht, wie Dr. Jac. P. Thijsse den Gesang des Zebrafinken im Speziellen beschrieben hätte, aber als ich mit meiner Doktorarbeit angefangen habe, war ich persönlich nicht besonders beeindruckt. Je länger ich mich jedoch damit beschäftigte, desto mehr interessante Aspekte habe ich entdeckt. Außerdem macht es Spaß, das Verhalten der Zebrafinken zu beobachten.

Ziel meiner Doktorarbeit war es, einen besseren Einblick in die unterschiedlichen Aspekte des Vogelgesangs, des Lernprozesses und des Sozialverhaltens der Zebrafinken zu bekommen. All diese Aspekte sind Teil eines komplexen Systems, das mit einem Puzzle verglichen werden kann: erst wenn alle Stückchen an ihrem Platz liegen, entsteht ein klares Bild. Ich möchte definitiv nicht behaupten, dass ich dieses Bild komplettieren kann, aber vielleicht kann ich mit dieser Dissertation ein paar kleine Stückchen beitragen.

Voorwoord

“Hier is nu de Vogelzang. Alles wat lieflijk is en welluidend. Laat ons dit alvast vasthouden voor het voorwoord.”
Dit is de aanhef van een brief, waarmee Dr. Jac. P. Thijsse in maart 1938 het manuscript voor een Verkade-album met de naam ‘Vogelzang’ inleverde, dat uiteindelijk in 1965 gepubliceerd werd (Vogelzang. Dr. Jac. P. Thijsse 1938. Published by Koninklijke Verkade Fabrieken N.V. Zaandam 1965). Verkade is een Nederlands bedrijf dat vooral bekend is voor beschuit, koekjes en chocolade.

De beroemde albums begonnen als reclame-actie. Bij verpakte koeken en in bussen beschuit werden plaatjes bijgesloten die in de verzamelalbums ingeplakt konden worden. De meeste albums hadden biologische thema’s en droegen ertoe bij de kennis van en de betrokkenheid bij de natuur onder de bevolking te vergroten.

Het hier geciteerde album gaat over vogelzang en beschrijft hoe mooi de Nederlandse inheemse soorten zingen. Ik weet niet hoe Dr. Jac. P. Thijsse de zang van Zebravinken zou beschrijven, maar toen ik met mijn promotie-onderzoek begon was ik er persoonlijk niet erg van onder de indruk. Hoe meer ik me er echter mee bezighield, hoe meer interessante aspecten ik eraan ontdekt heb. Bovendien is het erg leuk het gedrag van zebravinkjes te bestuderen.

Het doel van mijn promotie-onderzoek was meer inzicht te krijgen in verschillende aspecten van vogelzang, het leerproces en sociaal gedrag van zebravinken. Dit alles maakt deel uit van een complex systeem, dat met een puzzle te vergelijken is: pas als alle stukjes op hun plek liggen ontstaat een duidelijk beeld. Ik wil zeker niet suggereren dat ik dit beeld compleet kan maken, maar misschien kan ik met dit proefschrift een paar kleine stukjes bijdragen.

Chapter 1

Introduction

1.1 Communication & Vocal Learning

1.1.1 Communication

In our modern society, communication plays a crucial role. Novel communication mechanisms (e-mail, sms, facebook, twitter) have become available during the last few years and technology is steadily being advanced and improved. With this technological development, new problems arise as well, for although it seems obvious, effective communication is not as easy as it seems. Regardless of the form, be it written documents, vocal communication, or electronic data transmission, communication always takes place on more than one level at the same time.

This was already acknowledged by the Greek philosopher Aristotle. In his work "Rhetoric" (cited by Goff *et al.* 2010) he identified the elements necessary for a speaker to make his audience "get the message". He distinguished between three elements: Logos; Pathos; and Ethos. Logos (which literally means "word") represents the content-level: facts, arguments and logic that are conveyed through language. Pathos (literally "suffering") represents the emotional level and includes para-verbal and nonverbal signals like intonation, mimics, gestures, etc. The information conveyed on this level determines how the information from the logos-level should be interpreted. The final level, Ethos (custom, habit, character, etc.) contains context-information and is therefore the foundation of successful communication: both other levels need to be carried by a general understanding, a common knowledge base between speaker and audience (fig. 1.1).

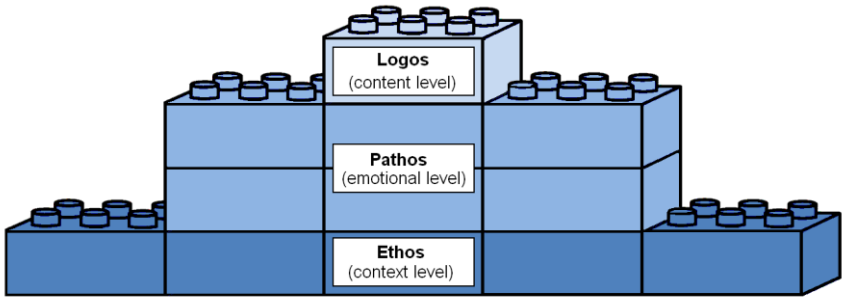

Figure 1.1: graphical representation of the communication model according to Aristotle.

Not the literal message that is sent, but how it is interpreted by the receiver is the message that counts in communication. This can be illustrated with a famous quote by Albert Einstein: "Das größte Problem mit der Kommunikation ist die Illusion, dass sie stattgefunden hat". It means that the biggest problem with communication is that people think that it has taken place when facts are exchanged on the "logos"-level. Too often the other levels of communication are neglected, which could lead to serious misunderstandings (Goff *et al.* 2010).

1.1.2 Social Aspects of Vocal Communication

The critical factor that gives communication its meaning is social interaction. Without the social aspects, information that is being sent on the "Logos-level" is useless. In order to understand how successful communication works, it is crucial to appreciate these social aspects and the context in which communication takes place.

This already starts at an early stage of human development, where social input is essential for speech acquisition. The ability to produce sounds is innate to us, but in order to use these sounds in a structured way (speech) so that they can be used for information

transmission, needs to be learned. Human speech, which forms the basis of communication, is acquired in a process of vocal learning (Kuhl 2007).

1.1.3 Vocal Learning

Although vocal learning is quite rare in the animal kingdom, it is not unique to humans. Some other mammals, e.g. bats, cetaceans and elephants, are also shown to have the capacity for vocal learning (Jarvis 2006), but the most well-known examples of vocal learners are birds. However, even among them it is not self-evident to have the capacity vocal learning, which so far has only been found in hummingbirds, parrots and songbirds (Catchpole & Slater 1995; Jarvis 2006).

Across continents and cultures, human children reliably learn speech. The process of vocal learning already starts before birth, when the baby starts to recognise the voice of its mother, and proceeds postnatal with listening, babbling and eventually speaking. Social influences on this process are indispensable for vocal development and can be distinguished into two factors, as defined by Locke and Snow (1997): "*social stimuli that are universally available to normally developing infants and social stimuli that are related to culture, social class or other factors that vary across infants*".

Like human infants, other vocal learners go through a sensitive phase in early life, during which they are most capable of learning (Doupe & Kuhl 1999). Although many species are able to learn after this phase, it usually becomes increasingly difficult with age. In humans, this is demonstrated for example when we start learning a foreign language at later age (Walsh 1979). Some species lack the ability for vocal learning after the sensitive phase altogether. This makes them to age-limited learners, also called closed-ended learners (Brainard & Doupe 2002).

1.1.4 Vocal Learning in Birds

Among all species that are capable of vocal learning, birds have been most thoroughly investigated. Most studies focus on vocal learning within species, but several cases of between species vocal learning are documented as well. In such cases, the importance of social factors is probably even more striking. A good example is a study by Baptista & Petrinovich (1986), in which fledgling hand-reared white-crowned sparrows were exposed to adult song sparrows and strawberry finches: Instead of producing a species-specific white-crowned sparrow song, these fledglings actually learned the song of their tutors. Some species, like starlings or parrots, are even capable of learning through social interactions with humans. Probably the best known example of an animal that has successfully learned to imitate human vocalisations and – to some extent – use human language (English) in a functional way is grey parrot Alex (Pepperberg 1997).

1.1.5 The Zebra Finch as Model Species

Birdsong and vocal learning in songbirds are studied because they are interesting in itself, but also because of the parallels between song learning and speech acquisition mentioned before. Both processes take place in a social setting and social input is necessary for vocal learning. Furthermore, the result of vocal learning, be it speech or song and calls, only gets its meaning through social interactions. Only if an adequate social setting is provided, successful communication is possible.

Over the past 50 years, Zebra Finches have been used in numerous studies on behavioural, molecular and electrophysiological substrates of vocal learning (reviewed by

Derégnaucourt, 2011). The Zebra Finch is a good model for studying vocal learning because it is easy to keep and breed in captivity, males produce only one song motif, and much is known already about its physiology and behaviour. For these reasons, the Zebra Finch was also chosen as a model species for the current study.

1.2 Zebra Finches

1.2.1 General Description

Zebra Finches are small passerines, belonging to the family Estrildidae. They are sexually dimorphic, but both males and females have a remarkable black and white banded tail and owe their name to this special feature. The scientific name *Taeniopygia* comes from the Greek words tainia, which means stripe or band, and pyge, which means tail. Wild-type birds are grey with whitish bellies and orange-red legs and beaks. Both males and females are around 10 cm long and have markings on both sides of the face: a small vertical white stripe next to the beak and a larger vertical black stripe underneath the eye. Males can be recognised by their additional chestnut coloured cheeks, chestnut-white checked flank patterns and the black-striped badge on their breast (fig. 1.2). Zebra Finches feed on seeds, which they usually collect on the ground, and live in groups (Zann 1996).

Figure 1.2: Wild-type plumaged Zebra Finch pair in an experimental aviary. The male is clearly recognisable by the chestnut coloured cheeks, checked flanks and the black-striped breast badge. Usually the beak is also a bit redder than that of the female. Female Zebra Finches are less conspicuously coloured. Both sexes are the same size. The numbered metal rings on the right legs give information about where and when the bird was bred and coloured leg rings facilitate individual recognition during behavioural observations.

1.2.2 The Origin of the Zebra Finch

There are two sub-species of Zebra Finches (*Taeniopygia guttata*) that are found over a wide range of continental Australia (*Taeniopygia guttata castanotis*), and parts of Indonesia and coastal areas around the continent of Australia (*Taeniopygia guttata guttata*; Zann 1996). Both sub-species are highly social animals, and group life is organised mainly by means of vocalisations. The Zebra Finch (*Taeniopygia guttata*) is one of the world's most popular cage birds, ranking 3rd behind the Budgerigar and Canary (www.zebrafinch-society.org). It is not exactly documented when the species first came to Europe, but it became known to science at the start of the 19th century (Zann 1996) and regular breeding in captivity was reported in the book "Die Gefiederte Welt" (1872). By the time the export of wild Australian Zebra Finches was prohibited (in 1962), they were already well established in the western world (Bosch *et al.* 2010; Zann 1996).

1.2.3 Zebra Finches in Captivity

Zebra Finches are very popular with hobbyists, since they are easy to keep and breed in captivity, and display a variety of genetically determined external traits and colour morphs. In Europe and the USA, several "Zebra Finch Societies", associations of Zebra Finch breeders and enthusiasts were founded in the second half of the 20th century, and special clubs also exist in e.g. South Africa, Canada, New Zealand, and of course Australia (http://zebrafinch.info/clubs). However, Zebra Finches are more than good pets: they are also the avian model of choice for scientific research on e.g. social behaviour, neurobiology and song learning (Derégnaucourt 2011; Zann 1996).

Although Zebra Finches have been held in captivity for decades, domestic Zebra Finches still closely resemble their wild cousins in many ways. Subtle differences are observable in traits like body size and song. The weight of free-living adults ranges between 10-17.5 g and there are no real size differences between males and females (Zann 1996). Through active selection by breeders, captive Zebra Finches are nowadays up to 25% bigger than their wild relatives (Bosch *et al.* 2010; Tschirren *et al.* 2009). Vocalisations of captive populations are similar to those of wild populations and the number of syllables per song (song complexity) does not differ significantly between domesticated and wild birds, although the former sing more rapidly and therefore have shorter mean song durations (Zann 1993a, b, 1996). However, most domestic Zebra Finches still show wild-type plumage (grey), clutch size and general social behaviour, and can be stimulated to start breeding at any time of year.

1.2.4 Housing Conditions

Usually Zebra Finches are held in aviaries where they are confined to a limited space. In order to keep captive Zebra Finches in optimal condition and to maximise fitness, the right housing conditions are very important. Housing conditions can have direct and indirect effects on various aspects of Zebra Finch physiology and behaviour. Breeders and hobbyists therefore pay a lot of attention to the design of cages and aviaries, especially with respect to lighting, ventilation, heating and nest boxes. For keeping Zebra Finches as laboratory animals, European standards have been determined and laid down in Animal Welfare Acts. According to current European standards for keeping Zebra Finches as implemented in Germany, groups of 13-20 animals can be held in aviaries of at least 4 m^3 (2m^2 surface area, 2 m high). For larger colonies, the aviaries need to be 0.05 m^2 larger per additional bird. (EU 2007).

Housing conditions can have effects on Zebra Finch physiology, fitness and behaviour. However, little is known about the minimum volume of space that is actually required per individual, optimal animal density, or the optimal group size. This is remarkable, since this local population density can have effects on a wide range of traits both in the wild and in aviaries. Studies on the effects of population density in captivity and aviary conditions on physiology and behaviour have so far only been carried out in commercially bred species like chicken (*Gallus domesticus*: Campo *et al.* 2005; Degen *et al.* 2003; Estevez & Leone 2008), but not in Zebra Finches.

1.3 Social Behaviour

1.3.1 Living in Groups

Many species, especially those feeding on transient food sources like seeds or fruits, live in groups. The main advantages of group life are increased likelihood of finding resources, and protection from predators through increased vigilance (more eyes see more) and dilution effect (reduced chances of predation to the individual). Although the advantages of group life clearly outweigh the disadvantages, there are some downsides like increased direct competition or competition through interference. The latter occurs when the availability of resources to a group member is reduced as a result of the behaviour of nearby companions (Krebs & Davies 1993).

Zebra Finches (*Taeniopygia* guttata) are highly social animals (Blakers *et al.* 1984; Zann 1996) that roost and breed relatively close together in stable colonies, which may congregate into larger foraging flocks (150-350 birds) during daytime. Overall population density is usually limited by food availability (Zann 1996), like in Seychelles Warblers (Brouwer *et al.* 2009), and Cliff Swallows (Brown *et al.* 2006). However, large variation is possible in local population density (Brown *et al.* 1990; Zann 1996). Group size and local population density are usually determined by food availability and predation risk, although for Zebra Finches, the availability of water is probably at least as important (Immelmann 1962; Zann 1996). In dry periods, they sometimes travel great distances to find water and tens of thousands of birds can gather around single water sources (Zann 1996). Pairs and family groups keep together even within such large congregations and social structures are maintained by means of vocalisations (Dunn & Zann 1997; Zann 1996).

1.3.2 Agonistic Behaviour

The social life of Zebra Finches is usually rather harmonious, although aggression is not uncommon. Zebra Finches are known to fight over food, nest material, mates, and favourable positions for perching, roosting and breeding (Caryl 1975; Evans 1970; Immelmann 1962; Zann 1996), but aggression over food is rare in captivity (Evans 1970). Aggression levels are usually low during non-breeding periods both in the wild and in aviaries (Case 1986), but increase at colony establishment, pair formation and nest defence (Case 1986; Ikebuchi & Okanoya 2006). Zebra Finches are not territorial, but they are known to defend a small space (ca. 20 cm in diameter) around their own nest site (Ikebuchi & Okanoya 2006). Both pair members work together to build the nest: the male identifies suitable nesting sites and collects building material, whereas the female decides where the nest is actually built (Zann 1996). They fight together as a team to defend their nest and in doing so; they are known also to win against higher ranking individuals. Furthermore, they defend their partner against approaches by same sex rivals (Zann 1996).

1.3.3 Social Dominance

In many group living species, clear social orders exist, which facilitates group life and reduces levels of aggression (Chase *et al.* 2002; Dewsbury 1982; Ellis 1995; Poisbleau *et al.* 2005; Rowell 1974). Social orders, also defined as dominance hierarchies, occur both in nature and in the laboratory (Chase *et al.* 2002). Many definitions of dominance were formulated over the years, but most of them have in common that they refer to agonistic behaviour (Drews 1993). Dominance hierarchies are typically established through competitions between group members (usually pairwise) and are more or less stable (Chase

1974). The animals within a group probably do not have to measure themselves in agonistic interactions with all other group members, but may use transitive inference instead (Bond *et al.* 2003; Peake *et al.* 2002). Paz-y-Mino *et al.* (2004) for example showed that Pinyon Jays are able to draw sophisticated inferences about their own dominance status relative to that of strangers, based on observed interactions with known individuals.

For the individual it is worthwhile to compete for dominance, since a high rank is often associated with priority access to resources (Banks *et al.* 1979) and increased reproductive success (Dewsbury 1982; Ellis 1995). Furthermore, dominance is related to net fitness (Bryant & Newton 1996), although the extent to which this is the case differs between species (Craig 1986).

Dominance is not a static trait, and its predictability is therefore neither perfect nor permanent (Chase 1982; Drews 1993). However, it is often associated with physiological and behavioural traits like body size (Robinson-Wolrath & Owens 2003), age, sex, weapons, coloration (Balph 1979; Bryant & Newton 1996), song (Dufty 1986; Spencer *et al.* 2004), personality (David *et al.* 2011; Fox *et al.* 2009; Lathi 1998), aggressiveness (Masure & Allee 1934) and hormones (Creel 2001; Poisbleau *et al.* 2005).

The classic example of a linear dominance hierarchy in a group of social animals is the pecking order in chicken (Schjelderup-Ebbe 1922), which is usually related to individual developmental state (Rushen 1982) and/or testosterone levels (Bennett 1940; Shoemaker 1939). However, the probability of linear hierarchy decreases with increasing group size (MestertonGibbons & Dugatkin 1995).

In wild Zebra Finches, Zann (1996) did not observe linear dominance orders. However, in captive Zebra Finch populations, there are indications that some individuals are more dominant than others, and that higher ranking birds can be identified by the relatively high number of agonistic interactions that they induce and win (Clodius 2011; Evans 1970; Zann 1996). More aggressive animals initiate and win more fights, for example over favoured (high) perches and nest sites (Zann 1996), and form a roughly linear dominance hierarchy (Clodius 2011; Evans 1970). Less dominant birds yet may win against higher ranking individuals when defending their own nests (Case 1986; Zann 1996). If food is limited, dominant birds show the highest overall daily mass gains, although subordinates maintain higher fat reserves at dawn (Cuthill *et al.* 1997), but see Beauchamp (2006).

1.4 Reproduction

1.4.1 Pair Bonding

Zebra Finches form strong pair bonds (Butterfield 1970; Immelmann 1962; Silcox & Evans 1982; Zann 1977, 1994), which are at least semi-permanent in captivity (Butterfield 1970), but usually for life under natural conditions (Immelmann 1962). In captive birds, it was shown that artificial pair separation causes stress (increased corticosterone levels, altered behaviour), which is relieved immediately upon reunion (Remage-Healey *et al.* 2003). Pair members are usually identified as those that clump together and allopreen one another (Zann 1996). At least in captive birds, artificial pair separation causes stress (increased corticosterone levels, altered behaviour), which is relieved immediately upon reunion (Remage-Healey *et al.* 2003). Pair members are usually identified as those that clump together and allopreen one another (Zann 1996). When one pair bond member dies, which is not uncommon since mortality rates are high (around 67%: Zann 1996), the bird that is

left behind re-mates rather quickly (Zann 1997). The maximum life span of domesticated Zebra Finches held under optimal conditions is 5-7 years (Burley 1985) and wild Zebra Finches hardly ever reach the age of 5. To compensate for high mortality rates, females are able to lay their first egg around day 60 and day 90 in wild and domestic Zebra Finches respectively (Zann 1996), whilst sexual maturity is reached at around day 100 post hatching in females and a bit earlier in males (Bosch *et al.* 2010; Zann 1996).

Mate preferences are displayed by both sexes, but usually the females decide whether a pair bond is established or not (Zann 1996). Although mate choice is initially based on physiological traits like body size, colour morph and song production (Ikebuchi & Okanoya 2006; Riebel 2009), pair formation is determined by social interactions and pair members can be identified as those birds sitting together (clumping) and allopreening (Zann 1996).

1.4.2 Breeding Cycle

Zebra Finches are opportunistic breeders, capable of breeding at any time of the year when conditions are favourable, which is usually immediately after rainfall (Zann 1996). They start building nests right after rainfall so they can use the (usually) short period when vegetation is flourishing to feed their offspring (Bosch *et al.* 2010; Zann 1996). Zebra Finches in captivity can easily be stimulated to breed by providing them with nest material and green crop (fruit, vegetables: Bosch *et al.* 2010).

Clutch size ranges from 2 to 7, but a typical clutch consists of 5-6 eggs and is incubated by both the male and the female. On average, chicks hatch after 13 days of incubation, fledge at day 17-20 post hatching, and become independent from their parents when they have reached the age of 35 days (Birkhead *et al.* 1989; Boruszewska *et al.* 2007; Zann 1994, 1996). Some developmental stages of juvenile Zebra Finches are shown in fig. 1.3.

Figure 1.3: First stages of Zebra Finch development. Eggs – ca. 4 days post hatching– ca. 8 days post hatching – ca. 14 days post hatching. Chicks are dyed in order to facilitate individual recognition until they are large enough to be ringed.

1.4.3 Monogamy & Extra Pair Copulation

Zebra Finches are regarded as monogamous birds, although a number of studies show that forced and unforced extra-pair copulations (EPC) occur in both free-living (Birkhead *et al.* 1988a) and captive populations (Birkhead *et al.* 1988b; Burley *et al.* 1994; Houtman 1992; OlivaPurdy & Harding 1997). Numbers of resulting extra pair offspring (EPO) are generally low in wild populations (2.4%: Zann 1996; 3.3%: Birkhead *et al.* 1990; 1.6%: Griffith *et al.* 2010), but a fair amount of intra-specific brood parasitism, i.e. females depositing eggs in the nest of an unfamiliar pair, is found (9.8%: Birkhead *et al.* 1990; 1.6%: Griffith *et al.* 2010). In aviary studies, significantly higher numbers of EPO are found (Birkhead *et al.* 1989), sometimes as high as 27% of total offspring (Burley *et al.* 1996). Brood parasitism also

seems to be a frequent phenomenon in captive populations, with highly consistent individual differences between females laying exclusively in their own nests (pure non-parasitic strategy) and those laying eggs in both the own nest and the nest of another pair, thus following a mixed strategy (Schielzeth & Bolund 2010).

Although forced copulation is possible and less rare than expected, both in captivity and in the wild (Birkhead *et al.* 1988a; Birkhead *et al.* 1988b; Burley *et al.* 1994; Houtman 1992; OlivaPurdy & Harding 1997), females appear to control the number and timing of copulations within and outside the pair bond (Zann 1996). Furthermore, Forstmeier (2007) found that individual female Zebra Finches intrinsically differ in readiness to engage in EPC.

Zebra Finches are not the only species that engage in extra-pair copulations (EPC) and produce extra-pair offspring (EPO); in fact it is quite common among socially monogamous birds (Dias *et al.* 2009; Westneat & Stewart 2003). Males and females form monogamous pair bonds that last for at least one breeding season in about 90% of all bird species (Alcock 1998). However, Schuiling (2003) states that monogamy in general does not exclude 'genetic promiscuity' (i.e. EPC resulting in EPO). Typically around 10% of total offspring can be identified as EPO (e.g. Cory's Shearwater: Bried *et al.* 2010); Sedge Warbler: Buchanan & Catchpole 2000; Bluethroat: Fossoy *et al.* 2006; and Bullheaded Shrike: Yamagishi *et al.* 1992), though numbers can be as low as 1.7% (Oystercatchers: Heg *et al.* 1993) and as high as 50% (Blue-black Grassquits: Carvalho *et al.* 2006).

Butterfield (1970) stated: *"… it can be said that the duration of the (pair) bond is dictated to a large extent by selection pressures arising from the varying predictability of environmental conditions which, through their effects upon physiological mechanisms and/or social systems, ensure that adaptations arise permitting maximum use of favourable breeding conditions*". This suggests that Zebra Finches may be monogamous because this ensures optimal fitness in the natural habitat of wild populations. If this is true, it is well possible that Zebra Finches adopt different strategies in different environmental conditions.

The differences in numbers of EPO between wild and captive populations may be an indication for the existence of different reproductive strategies (Alcock 1998; Butterfield 1970). Although these differences could also be due to effects of aviary confinement and domestication (Zann 1996), or intensity of mate guarding (Arcese 1989; Birkhead *et al.* 1989; Dias *et al.* 2009), it is interesting to study this phenomenon in more detail. In Dunnocks for example, reproductive strategies are found to vary from monogamy to polyandry or polygyny, or even polygynandry, according to environmental conditions (Davies & Lundberg 1984).

1.5 Stress

1.5.1 Stress and Hormones

Environmental conditions, like resource availability and weather conditions can have vast effects on the development, physiology and behaviour of individuals. Harsh environmental conditions are known to cause stress and have negative effects on various aspects of an individual's life. Other factors that can induce stress are disease, parasite load, predation pressure, social environment, etc. The term "stress" is widely used and accepted, but remains abstract. In a paper about stress in relation to livestock housing and transportation, Von Borell (2001) states: "*Stress is defined as a condition in an animal that results from the action of one or more stressors that may be of either external or internal origin. Whether a*

stressor can be considered as harmful depends on the way an organism is able to cope with a threatening situation as it regains a state of homeostasis. In that way, stress can be measured and monitored in terms of behavioural and physiological alterations that might be indicative for the individual's state of well-being."

Although this seems clear, it remains impossible to quantify absolute stress levels as such. Individuals rely on different biological mechanisms (behavioural, autonomic nervous, endocrine and immune) to elicit stress responses to cope with stress (Palme *et al.* 2005). The endocrine (hormonal) responses involve glucocorticoids like corticosterone (fig. 1.4). Changes in plasma corticosterone are commonly used as an indication for stress in many species of animals (Harvey *et al.* 1980; Harvey *et al.* 1984; Whatley *et al.* 1977; Wingfield *et al.* 1992).

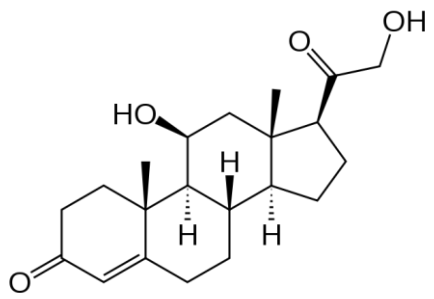

Figure 1.4: structural formula of corticosterone.

Corticosterone is a main glucocorticoid in birds and other species. Besides playing an important role in stress responses, it is involved in the regulation of metabolism and immune reactions. It is a steroid hormone that is produced in the cortex of the adrenal glands and reaches its target tissues via the blood (Palme *et al.* 2005). Usually it is released rapidly in response to stress situations. Although rapid short term increases in corticosterone levels may help an individual to cope with acute stress, chronic high levels may have negative consequences on fitness (rev. by Marra & Holberton 1998).

1.5.2 Corticosterone in Zebra Finches

So far, little is known about baseline corticosterone levels in wild Zebra Finches which might be because it is difficult to perform the procedure of capturing and taking blood samples within the required 3 minutes in the wild. Studies that have been carried out with captive animals show that baseline levels in blood plasma range between 0.5 – 10 ng/ml (Remage-Healey *et al.* 2003; Roberts *et al.* 2007; Wada *et al.* 2008), with high individual variation and usually with higher levels in adults than in nestlings (Wada *et al.* 2008). Nestlings growing up in larger broods (i.e. higher density in the nest) are usually smaller (body mass and tarsus length of) in comparison to nestlings from smaller broods (Gil *et al.* 2006), which could be related to differences in corticosterone levels as well.

Marra & Holberton (1998) found that American Redstarts in low-quality habitats display higher baseline levels of corticosterone and it is reasonable to assume a similar relationship in Zebra Finches. What is not known so far is whether increased local population density also has an effect on corticosterone levels.

1.6 Vocalisations

1.6.1 Vocal Behaviour

All birds are capable of vocal communication by means of calls, without ever having been into contact with adult conspecifics. These species-specific vocalisations can be described as innate and do not have to be learned (Doupe & Kuhl 1999). As mentioned before, the social life of Zebra Finches is organised mostly by means of vocalisations. When active they call

much of the time, except when feeding (Zann 1996). Immelmann (1962, 1969) was one of the first scientists who attempted to describe Zebra Finch vocalisations, but since he did not have modern sound recording equipment at his disposal, this was a tough undertaking. Nowadays we are able to use a range of sophisticated methods to record and analyse Zebra Finch vocalisations.

The most common way to get insight in the structure of, and differences between vocalisations, is to create a visual representation of a sound recording in a so-called sonogram. The horizontal axis of such a figure represents time, usually in ms, whereas the vertical axis represents frequency (usually in kHz). The intensity of the black bands in the figure shows how much energy is expressed in this frequency range. The lowest and usually strongest frequency-band is called the fundamental frequency; all overlaying bands are called harmonics (fig. 1.5).

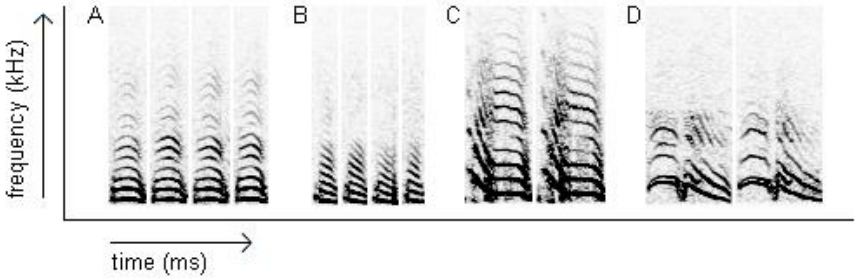

Figure 1.5: example sonograms. A: stack-call (unlearned, male and female), B: tet-call (unlearned, male and female), C, D: examples of distance call (learned, male only)

According to Zann (1996), Zebra Finches produce approximately ten distinct call types, which have an important function in communication within pairs, among families (parents and offspring), and between group members. The three most frequently uttered vocalisations are the “distance call”, “tet call” and “stack call” (fig. 4). On closer look, one also discovers that there is a lot of variation within call types and between sexes. Male Zebra Finches are capable of producing more vocalisations than females: in male Zebra Finches, innate vocalisations do not account for the whole repertoire of an individual. Certain call types (especially Distance calls, fig. 4C and D) contain learned elements, or are learned from adult tutors altogether (Zann 1996) and allegedly, different brain pathways are involved in the production of innate and learned vocalisations (Simpson & Vicario 1990).

Besides a repertoire of calls, male Zebra Finches also have their own song. Each song is unique and can be interpreted as individual signature (Zann 1996). The fact that only males sing is not uncommon among songbirds and song is assumed to have important functions in mate attraction and in many species also in territorial defence (Kroodsma & Byers 1991). Female Zebra Finches do not produce any learned vocalisations under natural conditions (Gurney & Konishi 1980) but they are able to recognise and distinguish between specific songs (Clayton & Prove 1989). When provided with several song motifs they show clear preferences (Riebel *et al.* 2009) and song thus plays an important role in the process of mate choice (Ikebuchi & Okanoya 2006; Riebel 2009).

Zebra Finches usually start their song with some introductory notes and then produce repetitions of a “motif”, which consists of 3 to 14 stereotyped “syllables”, with a mean of 6.75, in a fixed order (Derégnaucourt 2011, Zann 1993b). Figure 1.6A shows an example of Zebra Finch song.

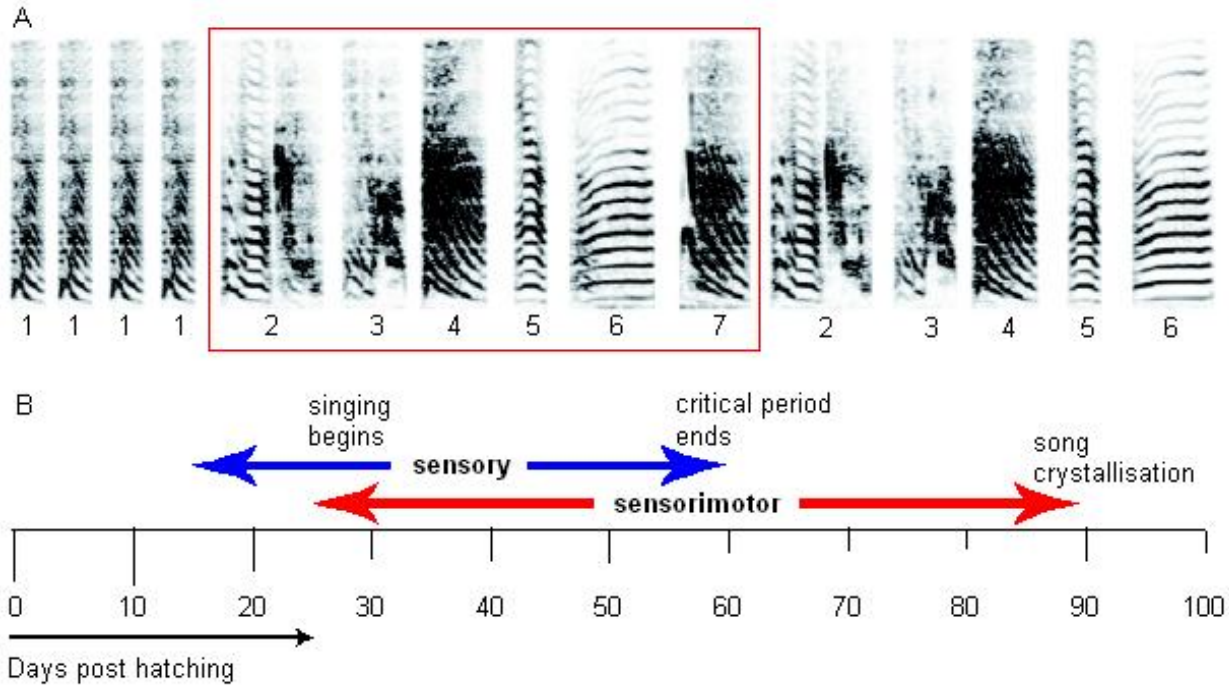

Figure 1.6
A) Example of a sonogram (graphic representation of Zebra Finch song) with time on the horizontal axis and frequency on the vertical axis. Zebra Finch song consists of distinct syllables, which are numbered 1-7. Syllable 1 is an introductory note and syllable 2-7 comprise the song motif, which is always produced in this fixed syllable sequence.
B) Schematic representation of the song learning process, after Doupe & Kuhl (1999). The horizontal axis represents time (in days post hatching) and the most important phases (sensory and sensorimotor) are depicted in the diagram. The process of song learning is completed with song crystallisation.

1.6.2 Song Learning

Zebra Finch song is not innate, like most call types, but has to be learned. Zebra Finches belong to the so-called “closed-end learners” (Brainard & Doupe 2002; Derégnaucourt 2011): they learn their song early in life and – under natural circumstances – are not able to change it anymore after it has crystallised (reviewed by Derégnaucourt, 2011). Juvenile Zebra Finches start learning by listening to adult tutors (sensory phase) around day 15 post hatching and from approximately day 25 they start producing so-called “subsong”, comparable to babbling in human infants, which indicates the onset of the sensorimotor phase. Both learning phases then overlap until day 60 post hatching, when the sensory phase (and therewith the critical period) ends. The sensorimotor phase ends with song crystallisation around day 90 post hatching (fig. 1.6B, after Doupe & Kuhl 1999). During the sensory and sensorimotor phase of song learning, juvenile Zebra Finches usually interact most with their parents. Juveniles are therefore assumed to learn from their fathers, although it is well possible that they learn from other males as well, as described in section 1.7.

1.6.3 What Happens in the Brain?

The fact that male Zebra Finches are able to learn and produce song is embedded in their brains and in the muscles controlling the vocal apparatus, which are larger and more developed than in females (Nottebohm & Arnold 1976; Wade & Arnold 2004). The brain regions that are most involved in song learning and production together form the so-called "song system" (McCasland 1987). Within the song system, an auditory pathway (song hearing, learning, feedback) and a vocal motor pathway (song production) can be identified. Both pathways and the brain areas involved are schematically represented in fig. 1.7.

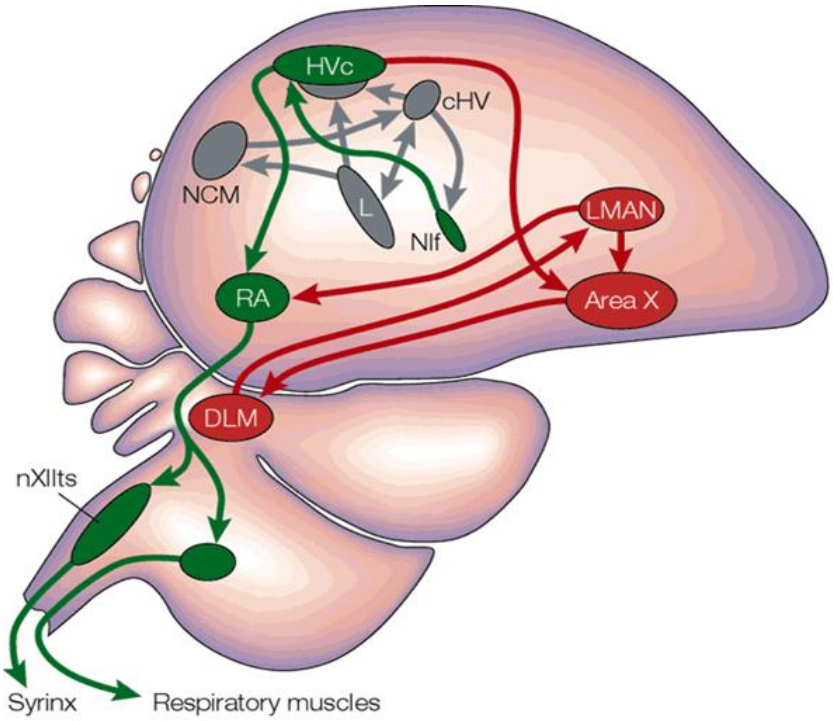

Figure 1.7: – The avian song system with the most important brain nuclei and auditory and motor pathways (Brainard & Doupe 2002). The green arrows indicate the motor pathway, the red arrows indicate the anterior forebrain pathway, and the grey arrows show the forebrain auditory inputs.

1.6.4 The Song Template: What Is It and Where Is It Stored?

The concept of an auditory template, or song template, was first formulated by Konishi (1965), as a basis for learning by imitation in songbirds. He showed that young White-crowned Sparrows who are allowed to listen to tutor song memorise an external song model and use this model as a template for their own vocalisations. Later, template learning was also recognised in Zebra Finches and other species. However, despite ample research efforts which have been made ever since Konishi posed his thesis, the template remains elusive (Adret 2004b).

Auditory regions in the brain, such as the NCM (fig. 1.7), are currently supposed to contain the neural substrate for the representation of tutor song and therewith the template (Bolhuis & Gahr 2006), but it remains unclear where the template is stored exactly. However, even if the brain region containing the template would be identified, the question as to what it is that the template codes for remains.

Does it represent the complete tutor motif, including syllables, syllable order and temporal structure? Or only parts of this? And in case the juvenile male is raised in a multi-tutor environment, does the template represent one tutor-song or the song of various tutors? Is it justified to speak of "the" template, or are there more? Another very interesting question is whether juveniles in a multi-tutor environment (social group) attempt to produce a perfect copy of tutor song, or rather try to create a unique, individual song.

1.7 Social Aspects of Song Learning

1.7.1 The Importance of Adult Tutors

Zebra Finch vocalisations convey social information and are learned in a social context. It is generally assumed that juvenile Zebra Finches need social interaction, defined as mutual or reciprocal action or influence, with (live) conspecific tutors, for successful vocal learning (Nelson 1997, Zann 1996). In Nightingales, strict imitation does not fully account for the acquisition of some learned song attributes: the repertoires of both free living and laboratory tutored birds include invented songs as well. However, invented songs are significantly more stereotypical than the songs of untutored birds, which underlines the importance of tutoring for successful song learning (Hughes *et al.* 2002). It is possible that this applies to other species as well, although it has to be noticed that song learning strategies differ between species. Juveniles that are not exposed to adult male song tutors during development produce vocalisations that are identifiable as species-specific song, but lack normal syntax and temporal organisation (European Starling: Böhner & Todt 1996; Zebra Finch: Price 1979). In Zebra Finches, this so-called untutored song (Williams *et al.* 1993) is composed of noisy, broadband notes and high-pitch upsweeps and is less stereotyped than tutored song (Derégnaucourt 2011). However, Feher *et al.* (2009) showed that wild-type song can be established within a few generations of Zebra Finches that descend from untutored ancestors.

Zebra Finches that are raised by their (foster) mothers incorporate female calls in their song when no male tutors are available (Eales 1987a). When presented with tutors of different species, they are also able to learn heterospecific song (Bengalese Finch: Eales 1987a; Immelmann 1969; Avadavats (Munia): Price 1979; Canary: Gehrold, Leitner & Derégnaucourt unpublished data). One of the first scientists to appreciate the need for (live) adult song tutors in order to produce “normal” song was Nicolai (1959). He performed tape-tutoring experiments with Bullfinches and found that in these circumstances juveniles are not able to exploit their song learning capabilities to the same extent as in the wild and produce poorer songs as adults. Later, similar results were also found for other species, including Zebra Finches (Derégnaucourt 2011).

Juvenile Zebra Finches that are for example isolated from live tutors, but exposed to either passive or active playbacks of tape-recorded tutor song, display a high inter-individual variability in learning success. However, none of these birds is able to produce a perfect copy of the tutor song (reviewed by Derégnaucourt, 2011). Similar results are achieved with juveniles that are able to interact vocally but not visually with a live tutor: they make inaccurate copies of tutor song and/or incorporate elements of song they have heard before isolation (Eales 1989). Visual stimulation seems to be an important factor for successful learning from a tutor, but apparently it is not decisive. Adret found that blindfolded birds that are allowed direct (physical) contact to their tutor and siblings imitate tutor song (Adret 2004a). However, he also found that Zebra Finches who are kept separately in single cages at 50 cm distance from their tutor failed to imitate his song (Adret 1992).

Although these studies offer a simplified representation of reality, they have made valuable contributions to our understanding of the process of vocal learning in Zebra Finches. As stated before, vocal learning in wild populations takes place in a complex social environment and vocalisations convey a certain meaning from sender to receiver in social interactions. Furthermore, there are indications that calls play a more important role in vocal learning than previously assumed (Mulard *et al.* 2010).

1.7.2 Tutor Preferences

Although juveniles in wild populations grow up in an environment with many potential song tutors, Zann (1990) found that they generally learn their song from their fathers rather than from other male tutors. In captivity, juvenile male Zebra Finches are also known to show clear tutor preferences. When presented with two tutors, they exclusively imitate one and show a preference for the father or the one who produces a motif that is similar to the father's (Böhner 1983; Clayton 1987; Jones & Slater 1996; Tencate & Slater 1991). Mann & Slater investigated why juvenile Zebra Finches that are presented with 2 (Mann & Slater 1994) and 6 (Mann & Slater 1995) adult tutors usually learn from their fathers, and identified 4 factors that play a role: 1) preference for the male with which they were housed before the sensitive phase; 2) preference for the male paired to the female who raised them; 3) preference for paired over single males; 4) preference for the same morph as the father (Mann & Slater 1994, 1995).

Evidence for the second and third factor was presented by Roper & Zann (2006), who found that juveniles choose the father over single unrelated males or unrelated males in company with their female partners. Another interesting observation is that most juveniles continue to associate more with siblings than with others after independence, and there is evidence that siblings that associate most closely develop similar song characteristics (Mann & Slater 1995; Volman & Khanna 1995).

Most of these studies however, were carried out in rather artificial settings, with offspring birds being exposed to a very limited number of tutors, whereas relatively little is known about tutor preferences in juvenile Zebra Finches growing up in a more natural multi-tutor environment. Although the results of Zann (1990) imply that they still prefer their father's song, it is well possible that they also, or even rather, learn their song from other tutors. This is for example the case in Savanah Sparrows (Wheelwright et al. 2008), who seem to prefer learning the song of their neighbours over the song of genetic or social fathers. Studying birds in a multi-tutor environment is more similar to the natural situation, and could provide valuable insights into the complex social relations and the process of song learning in a group of Zebra Finches. As indicated by Williams (1990), it is well possible that juveniles actively choose a song tutor, thereby preferring e.g. the male that is feeding them, which does not necessarily have to be their genetic father; the dominant male (implying the establishment of a dominance hierarchy within a population); the male that sings most or loudest; or the male with the highest fitness.

1.7.3 Methodological Challenges

Studying groups of freely behaving Zebra Finches in aviaries is challenging in many ways. First of all, the presence of multiple offspring probably has an effect on both song learning and tutor choice through social interactions with peers. Secondly, the conventional methods for analysing song learning are primarily suited for studying one to one similarity between

tutor and tutee song. Comparing all songs of all males in a group requires more sophisticated methods, which were custom-made and/or adapted for this study.

In order to study vocal interactions, continuous and simultaneous recordings of all individual male group members in a semi-natural environment were made in another experiment. Since this is a completely new procedure, carrying out this study was challenging. Making sure all equipment is working and all recordings are properly stored is difficult, but analysing the data is even more so. Specialised methods needed to be developed and some work is still in progress.

1.8 General Aims and Expectations

1.8.1 Outline

In my thesis, I mainly focus on the factors that influence the process of song learning and tutor choice in Zebra Finches. Furthermore, I investigate the social environment in which song learning and vocal communication take place, and the effects the various aspects of this environment may have. Data for this study were essentially collected in two main experiments, later referred to as experiment 1 and experiment 2. Experiment 1 consisted of four parts, which focussed on different aspects of the social life of Zebra Finches. In the final chapter of my thesis, I discuss all results and present a synthesis of relevant findings in the context of song learning and tutor choice. Furthermore, I present an outlook for further research.

1.8.2 Population Density (experiment 1A)

My first experiment was primarily designed to study the effects of population density. Based on pilot studies at the Free University of Amsterdam (Gahr, pers. comm.), I expected that increased local population density has a negative effect on body size and –mass and song complexity and that it causes elevated corticosterone levels, which may be an indication for stress. As already stated in section 1.3.1, food is usually the limiting factor for population density in wild populations. However, since food is provided *ad libitum* in aviaries, this cannot be an explanation for density effects in populations of animals that are held in captivity. In this experiment, I wanted to test whether local population density as such has an effect on Zebra Finch development, social behaviour, and stress as expressed by corticosterone levels.

1.8.3 Social Dominance (experiment 1B)

With the same animals as in the first experiment, I studied social dominance (part B). A recent study by David *et al.* (2011) showed that social dominance in Zebra Finches can be predicted by personality, with proactive individuals being more likely to become dominant. However, not much is known about other predictors of dominance in this species. The primary aim of this study therefore was to see if dominance can be related to specific traits like body size, song complexity (in males) and reproductive success. Furthermore, I wanted to find out whether dominant birds occupy higher perches as is the case in lizards (Radder *et al.* 2006; Zucker 1986).

In order to ascertain dominance hierarchies in Zebra Finches, most studies have used induced dyadic interactions (Clodius 2011; Ikebuchi & Okanoya 2006) or agonistic behaviour in a foraging context (Beauchamp 2006; Cuthill *et al.* 1997; David *et al.* 2011). The second aim of this study was to derive a dominance hierarchy from behavioural observations of spontaneously occurring agonistic interactions.

1.8.4 Behavioural and Reproductive Patterns (experiment 1C)

I observed differences in behavioural and reproductive patterns, which I investigated in more detail. I discuss whether it is possible that these different patterns in captive Zebra Finches reflect different reproductive strategies and use the data of the first experiment to illustrate this theory.

1.8.5 Song Learning and Tutor Choice (experiment 1D)

One of the main aims of my thesis was to find out whether juvenile Zebra Finches growing up in a more natural situation with many potential song tutors still prefer their father's song, or rather learn their song from other tutors. As shown in section 1.7, juvenile Zebra Finches are generally assumed to learn from their fathers, but so far, there is little empirical evidence that this is also the case in a multi-tutor environment. Furthermore, I wanted to investigate whether juveniles learn single song syllables or rather strings of syllables or complete song motifs (templates).

1.8.6 Vocal Interactions and Song Development in a Group (experiment 2)

So far there are only few studies that have focussed on calls in the context of vocal learning. In my second experiment, I therefore focus on vocal interactions through song AND calls, and attempt to test the hypothesis juvenile Zebra Finches learn most from those tutors with whom they have most vocal interactions. Evidence for this hypothesis is available from cage experiments (Clayton 1987; Eales 1987b; Immelmann 1969) but not yet from multi-tutor environments.

Especially analysing vocalisations of juveniles younger than 65 days post hatching proved complicated, which is why we continue to improve the methods and analyse the data of birds at younger ages. Here I use the opportunity to present the general methods and preliminary data that I was able to obtain within the scope of my thesis.

Chapter 2

Material & Methods

2.1 Aviary Setup

2.1.1 Experiment 1

The experimental setup consisted of 4 aviaries: 2 small aviaries (high density, $2m^3$; 1x1x2) and 2 large aviaries (low density, $8m^3$; 2x2x2), as shown in fig. 2.1. Food (commercial seed mix) and water were provided *ad libitum* in all aviaries. Vegetables and fruits (lettuce, carrots, cucumber, apple, orange) were provided twice a week.

Sitting space on the perches was limited to a total of 3 meters; divided over four perches of 75 cm. Perches were positioned at fixed heights and numbered accordingly: 1: 160 cm; 2: 130 cm; 3: 100 cm; 4: 70 cm. Each aviary was situated in a separate room with a constant temperature of 20°C and a light-dark cycle of 14:10 hours.

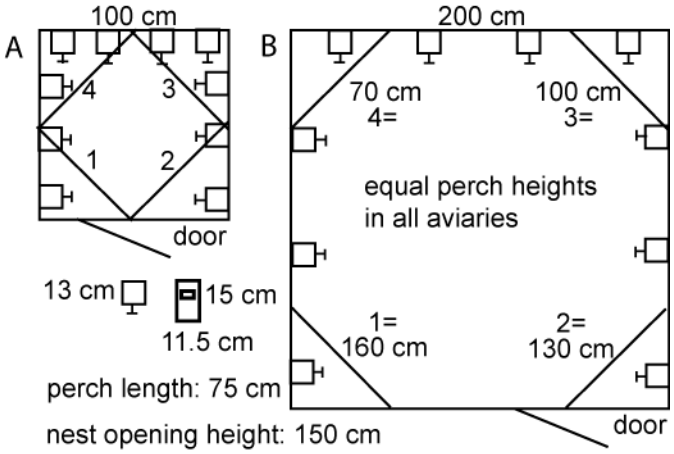

Figure 2.1: Aviary Setup. **A** High density aviaries had a volume of $2m^3$ (1x1x2), with 4 perches (75 cm each) positioned at 70, 100, 130 and 160 cm above ground. Nest boxes were equally distributed over 3 sides of the aviary, with the opening at 150 cm above ground. **B** Low density aviaries had a volume of $8m^3$ (2x2x2), with 4 perches (75 cm each) positioned in the same way as in high density aviaries. Nest boxes were again equally distributed over 3 sides, with openings at 150 cm above ground.

I introduced all birds to the 4 experimental aviaries at the same day (September 10th 2007). After a familiarisation phase of 10 days, in which the birds could get accustomed to new conditions and each other, regular behavioural observations started. On October 26th, 10 I installed empty plastic nest boxes on fixed heights, with the entrance at 150 cm above ground, and numbered from 1-10 (starting left from the aviary door). All nest boxes were equally distributed over 3 sides in each aviary. On the same day, I provided nest material (coir and cotton fibre) and the birds were allowed to build nests and breed.

2.1.2 Experiment 2

An experimental aviary of $4m^2$ and 2 m high was positioned in a closed room with controlled temperature and light conditions (20°C, 14:10 h light-dark cycle). Side panels were made out of mesh wire and the ceiling consisted of a Perspex plate. The aviary was prepared with 4 perches and 10 nest boxes, as in the large aviaries used in experiment 1. Four antennae were positioned on the ceiling of the aviary and connected to 4 receivers (AOR 8600). The receivers were connected to a 12 channel AD-converter and all equipment was positioned on a desk in the same room and connected to a pc with recording software (ASIO recorder).

I presented the birds with ad libitum nest material (coir), food (commercial seed mix) and water. Vegetables and fruits (lettuce, carrots, cucumber, apple, orange) were provided twice a week.

2.2 Birds

2.2.1 Experiment 1

40 male and 40 female unrelated Zebra Finches (*Taeniopygia guttata*) were obtained from a Dutch trader (Francis Kriesels), who held the birds in single sex groups before the experiment started. Upon arrival in the institute (August 2007), all animals were put together into a large aviary (2x4x2) for ca. 4 weeks. Prior to the experiment I weighed, measured, described and marked all birds individually by means of coloured leg rings (colour codes are found in the appendix). I took blood samples (2.4) for DNA-fingerprinting and recorded the song motifs of all males. No sex differences were found for tarsus length, wing length, and body mass.

I randomly assigned a female partner to all males and then put the pairs into a soundbox (Hartog *et al.* 2009) for 2 – 7 days in order to record their songs. When sufficient recordings were obtained (>10 files containing song), all birds returned to the large aviary. I randomly distributed the male-female pairs that had been together in a soundbox over the 4 experimental aviaries. In this way, 4 mixed-sex adult flocks with 10 potential breeding pairs per aviary were formed. However, only two of these pairs stayed together throughout the experiment, whereas most other birds formed pairs with different partners who either did or did not have previous soundbox-experience. This shows that pre-experimental experience was not relevant to ultimate pair bonding. Song analysis (2.7) revealed no differences in number of syllables and motif duration between the adult males in different experimental aviaries.

2.2.2 Experiment 2

On October 1st 2009 I introduced three established pairs of adult Zebra Finches who were known to have produced offspring together in a previous experiment into the experimental aviary. All birds were individually marked with coloured leg bands in order to facilitate visual recognition and I equipped the males of each pair with a telemetry microphone (2.6.2). They were allowed to breed at will and general behaviour, number of eggs laid and hatching success were monitored on a daily basis. At the end of the experiment, blood samples (2.4) were taken from all birds for DNA-analysis.

2.3 Breeding

2.3.1 Experiment 1

The birds were allowed to breed at will and in all four aviaries, birds started building nests and laying eggs as soon as nest boxes and nest material were provided. Progress was monitored daily by means of visual inspection. Per nest box, one breeding round was allowed: any eggs laid after the first chicks left the nest were removed and not taken into account.

I marked all eggs with nest and egg number. The first chick hatched on November 12th 2007 and the last on March 2nd 2008, although this really was a late arrival: of all the chicks that hatched, the median was November 28th, the first quartile November 16th and the third quartile December 15th. Hatchlings were marked with coloured ink and as soon as they were big enough, all got a closed steel ring with unique number. Later on, I provided

them with coloured rings to facilitate individual recognition and all birds were allowed to stay in the home aviaries.

At day 15, 60 and 100 post hatching, I measured and weighed all chicks, and took blood samples for DNA fingerprinting (2.4.2) and determination of plasma corticosterone levels (2.4.3). When all chicks were at least 100 days old, nest boxes were removed from the aviaries in order to prevent further breeding. At day 100 post hatching, I recorded the song of the male offspring (2.6.1), after which I returned them to their home aviaries.

2.3.2 Experiment 2

At the start of the experiment, the birds were allowed to breed at will and I monitored general behaviour, number of eggs laid and hatching success on a daily basis.

Eggs were marked and hatchlings were dyed for individual recognition. Around day 8 post hatching, I provided them with numbered metal rings and coloured leg rings for direct visual recognition. During the third week after hatching, secondary sexual characteristics (black badge, red cheeks) started to emerge and males could be identified. When the male offspring reached the age of 25 days post hatching and were considered strong enough, I also equipped them with a backpack telemetry microphone. As soon as 9 offspring males were identified, I removed the nest boxes from the experimental aviary and transferred younger offspring to another aviary in order not to interfere with the vocal development of the 9 focal offspring males. Although female offspring was not involved in the experiment, they were left in the aviaries with their family.

2.4 Blood Sampling

2.4.1 Collecting Samples

For blood sampling, the birds were individually caught from the aviary and brought to an adjacent room where the left wing vein was punctured with a needle (Sterican 0.45 x 25 mm). When samples were taken for corticosterone analysis, ~75 µl blood was collected in 2 micro haematocrit capillaries within 3 minutes after catching. When samples were intended for DNA analysis, a smaller volume of blood was collected. Samples were transferred from the haematocrit capillaries into individually marked standard Eppendorf tubes, and treated according to purpose.

I immediately stored the samples designated for corticosterone analysis on ice and brought them into the lab where they were centrifuged for 10 minutes at 6000 rpm. After this, I removed the plasma from the sample using a Hamilton's pipette and transferred it to a small, individually marked Eppendorf tube. All samples were stored in a freezer at -20°C until further use.

Samples designated for DNA analysis were diluted with ± 600 µl Queens Lysis Buffer and stored in a refrigerator.

2.4.2 Corticosterone Analysis (experiment 1)

One week before the nest boxes were introduced, we caught as many birds as possible within 3 minutes from each aviary (12, 14, 11 and 11 from aviary 1, 2, 3 and 4 respectively) and blood samples were taken in order to determine baseline plasma corticosterone levels. Samples had to be taken within 3 minutes since after that period corticosterone levels rise drastically, which is why not all birds were sampled. This is also the reason why not all birds

could be caught for sampling. After the experiment, when all offspring had reached adulthood, we again took samples (11, 12, 13 and 14 from aviary 1, 2, 3 and 4 respectively) and determined corticosterone levels.

Corticosterone was isolated from the blood plasma samples by direct radioimmunoassay (RIA), following Goymann *et al.* (2006). The lower detection limits of the standard curves were determined as the first value outside the 95% confidence intervals for the zero standard (Bmax) and was 6.15 pg/tube for the "start of the experiment"-samples and 3.09 for the "end of the experiment" and offspring samples. Intra-assay coefficients of variation were 6.8% (start of the experiment) and 7.7% and 9.8% (end of the experiment and offspring). The inter-assay variation was 7.5 %. If a sample concentration was below detection limit its value was set at that level.

2.4.3 DNA Analysis

For the birds from experiment 1, DNA was isolated from the blood samples and each individual was genotyped at 10 to 18 highly polymorphic microsatellite markers, as described in Forstmeier *et al.* (2007a). A DNA profile was obtained from all offspring that survived at least until day 15 post hatching, so that family relations could be determined with high confidence, by means of exclusion (Forstmeier *et al.* 2007a).

Samples from the birds from the second experiment were treated in the same way, although only 11 microsatellite markers were used to identify family relations in this smaller group of individuals.

2.5 Behaviour (experiment 1)

I observed all experimental birds individually from about 1 m distance of the aviary door, using a behavioural protocol (table 1). 15 minute observations were made at different times of day (08:00-18:00) on 7 occasions for each individual. Observation periods were equally spread over a period of 8 weeks, starting 10 days after the birds were introduced to the experimental aviaries.

During observation periods, I noted bird position in the aviary (table 2.1) and at the end of the experiment I calculated an average perching position for each individual. Birds were ranked accordingly: rank 1= highest average perching position; rank 20= lowest average position.

I used observational data on allopreening (preening the feathers of one bird by another), clumping (sitting together), directed song and mounting to identify pair bonds, since these behavioural patterns are described to be important for courtship or pair bond maintenance (Butterfield 1970; Silcox & Evans 1982; Zann 1977, 1996).

Both affiliate and aggressive interactions that occurred between dyads were entered into matrices. This resulted in a collection of matrices (aggressive behaviour; clumping; preening; directed song; mounting) for each aviary. I created a matrix called 'affiliate behaviour' by adding together the matrices 'clumping, 'preening', 'directed song', and 'mounting'.

Table 2.1: Protocol used for description of bird positions and behaviour in the experimental aviaries.

Positions in aviary		
op	on perch (1 – 4	
on	on nest (1 - 10)	
og	on ground	
of	on fence	
ow	on wing – flying around	
Behaviours		
A	attack/aggressive behaviour towards other individual	
D	defense from other individual	
P	s	preening oneself
	o	preening another individual (allopreening)
F	s	feeding oneself (eating)
	o	feeding another individual
S	u	undirected song
	d	directed song (towards other individual)
M	mounting (sexual behaviour)	
Z	sleeping	
Birds in close proximity of one another were scored as "sitting together"		

I used the "agonistic behaviour" matrix to calculate Landau's linearity index (h), a linearity index corrected for unknown relationships (h') and Kendall's coefficient of linearity (K), using MatMan 1.0 (De Vries 1993). These indices vary from 0 (absence of linearity to 1 (complete linearity). A linear dominance hierarchy was derived for each aviary and based on these hierarchies "behavioural ranks" were assigned to all individual birds. Furthermore, I calculated DCI (Directional consistency index), which range from 0 (completely equal exchange) to 1 (complete uni-directionality).

2.6 Sound Recordings

2.6.1 Song Recordings in Soundboxes (experiment 1)

Acoustically isolated boxes (soundboxes) equipped with microphones (as described by Hartog *et al.* 2009) connected to pc's with recording software (Sound Analysis Pro 2.062) were used to record the unique song of all males from the experiment. Only the in-files (raw data) were used for analysis. As described in section 2.2.1, I recorded the songs of all adult males before the experiment started. During the experiment, male offspring were transferred to soundboxes at day 100 post hatching. I presented them with an unfamiliar female of about the same age and from the same rearing condition (high/low density aviary) in order to stimulate song. After at least 10 files containing song were collected (usually after 2-3 days), the birds were returned to their home aviaries.

2.6.2 Continuous Recordings (experiment 2)

The three adult males and all male offspring >25 days post hatching were equipped with a telemetry microphone (Sparrow Systems microphone transmitter), weighing 1.3 gram incl. battery, which was integrated in a specially designed backpack that consisted of silicon tube and cotton bandage (fig. 2.2).

Each microphone had its own unique transmitting frequency, and the receivers in the room were tuned to these frequencies so that each channel could be attributed to an individual bird. The pc was programmed to continuously record all vocalisations produced between lights-on and lights-off and recordings were saved on a server until further use.

The batteries that supplied power to the telemetry microphones lasted max. 2 weeks before they had to be exchanged. For this purpose, we caught the birds from the aviary every other week. The experiment was set to end when all offspring had reached the age of 100 days post hatching.

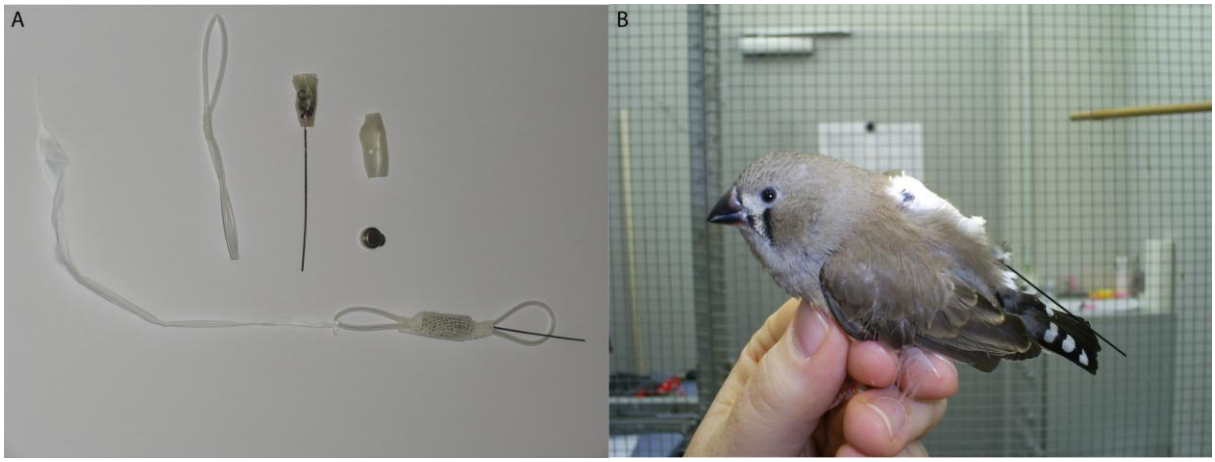

Figure 2.2. A) Microphone transmitter, silicon tubing, and battery, which together make up the essence of the backpack. The whole is then wrapped in bandages for protection, and a dot is made with waterproof marker in order to identify the side of the microphone that needs to be oriented away from the body. B) Juvenile Zebra Finch (ca. 25 days post hatching) wearing a backpack.

2.7 Song Analysis

2.7.1 Sonograms

I plotted Sonograms (graphic representation of audio signal, fig. 1.6A) for both the songs of the offspring and the adult males (tutors). In experiment 1, I counted the total number of "unique" syllables and the number of syllables per motif for each bird (adult and offspring), and determined mean motif duration (in ms) by averaging the duration of 10 randomly selected complete motifs. Introductory notes were excluded from analysis: only syllables that were obviously and consistently incorporated in the motif were taken into account.

2.7.2 Syllable Clustering

Ca. 25 files containing song (soundbox-recordings in experiment 1 and telemetry microphone recordings from a day at the end of experiment 2) were selected from the sound files produced by each animal. I only selected sound files that actually contained song syllables (selection through visual inspection), so that the amount of interfering noises (wing flapping, feeding, female calls, etc.) was minimised. The sound-files from experiment 1 (Sound Analysis Pro in-files) were max. 3 minutes long and ready to use for analysis, but the continuous recordings from experiment 2 needed to be prepared first. The long sound files were cut into smaller pieces by triggering on sounds and selecting records until 5 seconds after the end of the last sound.

I combined the song files of all birds (tutors AND offspring), and extracted the syllables from this set of files, hiding the identity of the individual that produced the particular syllables. For syllable sorting, I used a k-means clustering paradigm using 8 acoustic parameters. The resulting clusters were then attributed to the individuals that

produced them (fig. 2.3). Sorting software was written by René Jansen (Sound Explorer), and the file selection and syllable attribution software was written by Andries ter Maat.

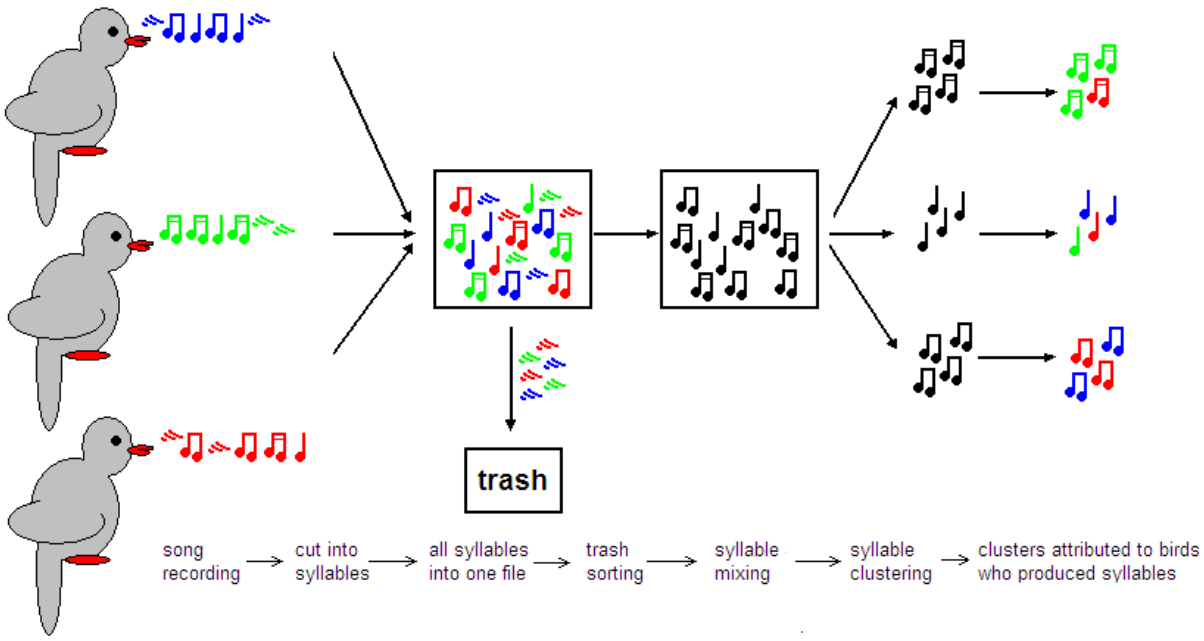

Figure 2.3: Schematic representation of the song analysis process.

All unique clusters of syllables could be attributed to either one or several birds. Since juvenile Zebra Finches are generally assumed to produce (near) perfect copies of tutor song, it was expected that all offspring syllables could be attributed to a tutor syllable.

2.7.3 Cluster Classification

In experiment 1 the clustering procedure resulted in ca. 75 clusters per aviary in experiment 1. Overall, around 58% of all clusters contained only syllables that were produced by tutors. From the other clusters, 17% contained syllables produced by a tutor and at least one offspring, whereas the other 25% contained syllables that were only produced offspring birds. Screening of these offspring clusters we found that most syllables looked similar to syllables that were produced by tutors. I thus assumed that these offspring syllables were learned from tutor syllables. However, in some clusters the similarity to tutor syllables was more obvious than in others and the extent to which the offspring syllables resembled tutor clusters could be categorised.

At this stage, five categories were defined to describe the syllables produced by the offspring birds as:

(1) real copies of tutor syllables – syllables that were indistinguishable from tutor syllables and were present in the same cluster as the tutor syllables;

(2) imitations of tutor syllables – syllables that were clearly similar to tutor syllables, but were present in separate clusters;

(3) variations on tutor syllables – syllables that were similar to tutor syllables, but clearly also had some individual characteristics and were present in separate clusters;

(4) elements of tutor syllables – syllables that were clearly similar to parts (elements) of tutor syllables, sometimes recombined with other parts: on first glance these syllables

looked unique and the similarity to tutor syllables only became clear after more thorough inspection. These syllables were present in separate clusters;
(5) new syllables – offspring syllables that did not resemble any tutor syllable and were present in separate clusters.

Together with my supervisor Andries ter Maat, I classified all offspring syllables to any of these five categories. Examples of all categories are shown in fig. 2.4 and fig. 2.5.

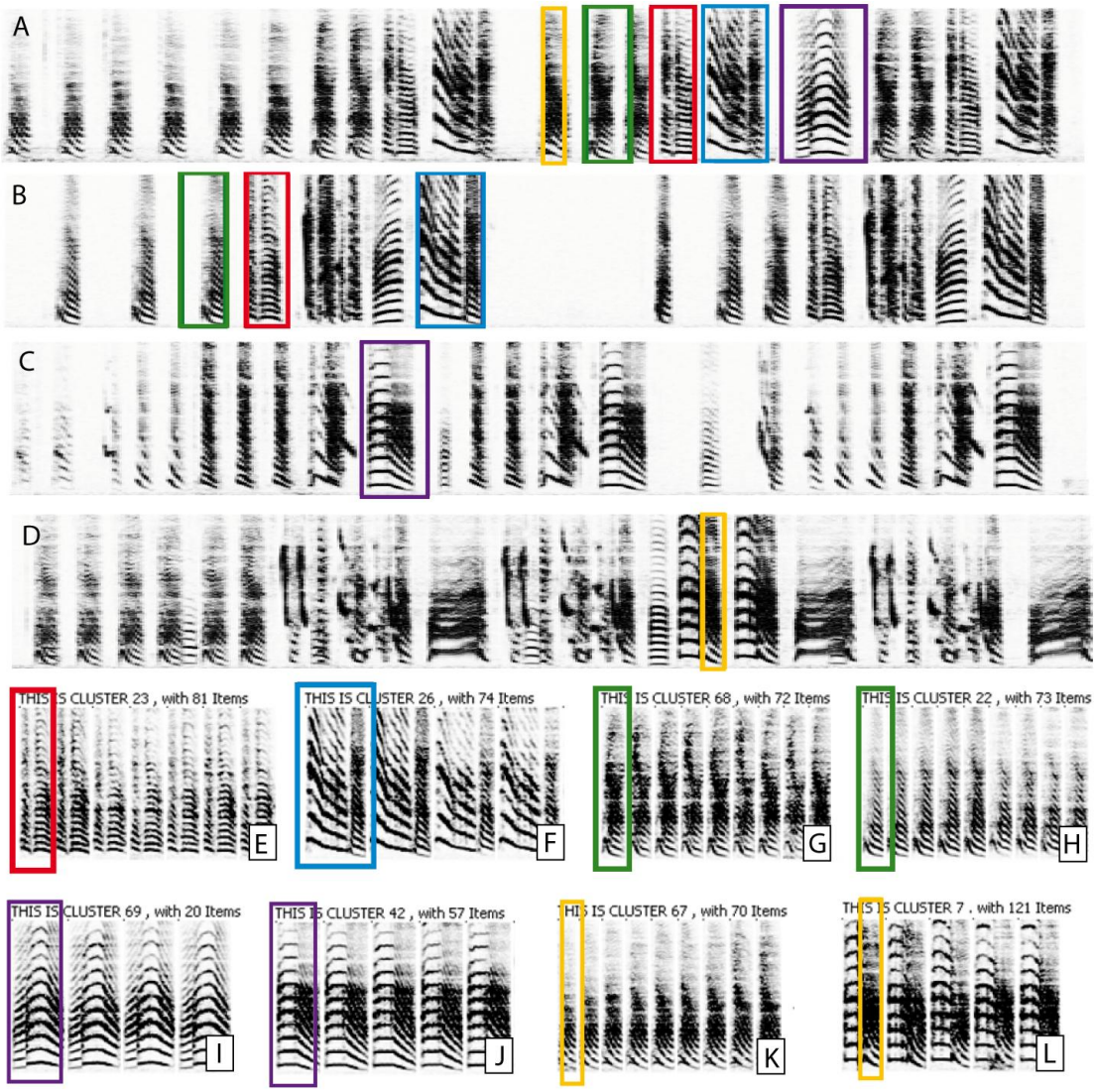

Figure 2.4: Example sonograms of song motifs and learned syllables from different categories in comparison to original motifs and syllables. This is a nice example of a bird that learned from more than one tutor. Panel **A** shows the sonogram of the motif of a juvenile Zebra Finch (>100 days post hatching) from aviary 2. Panel **B**, **C** and **D** show sonograms of tutor 1 (main tutor), 2 and 3 respectively. **E** and **F** show examples of category 1: copy. The juvenile shares these syllables with the tutor from whom they are learned (tutor 1). **G** and **H** show an example of category 2: imitation – G shows the offspring syllable, learned from H: the original tutor syllable (tutor 1). **I** and **J** show an example of category 3: variation – I shows the offspring syllable, learned from J: the original tutor syllable (tutor 2). **K** and **L** show an example of category 4: element – K shows the offspring syllable, learned from L: the original tutor syllable (tutor 3).

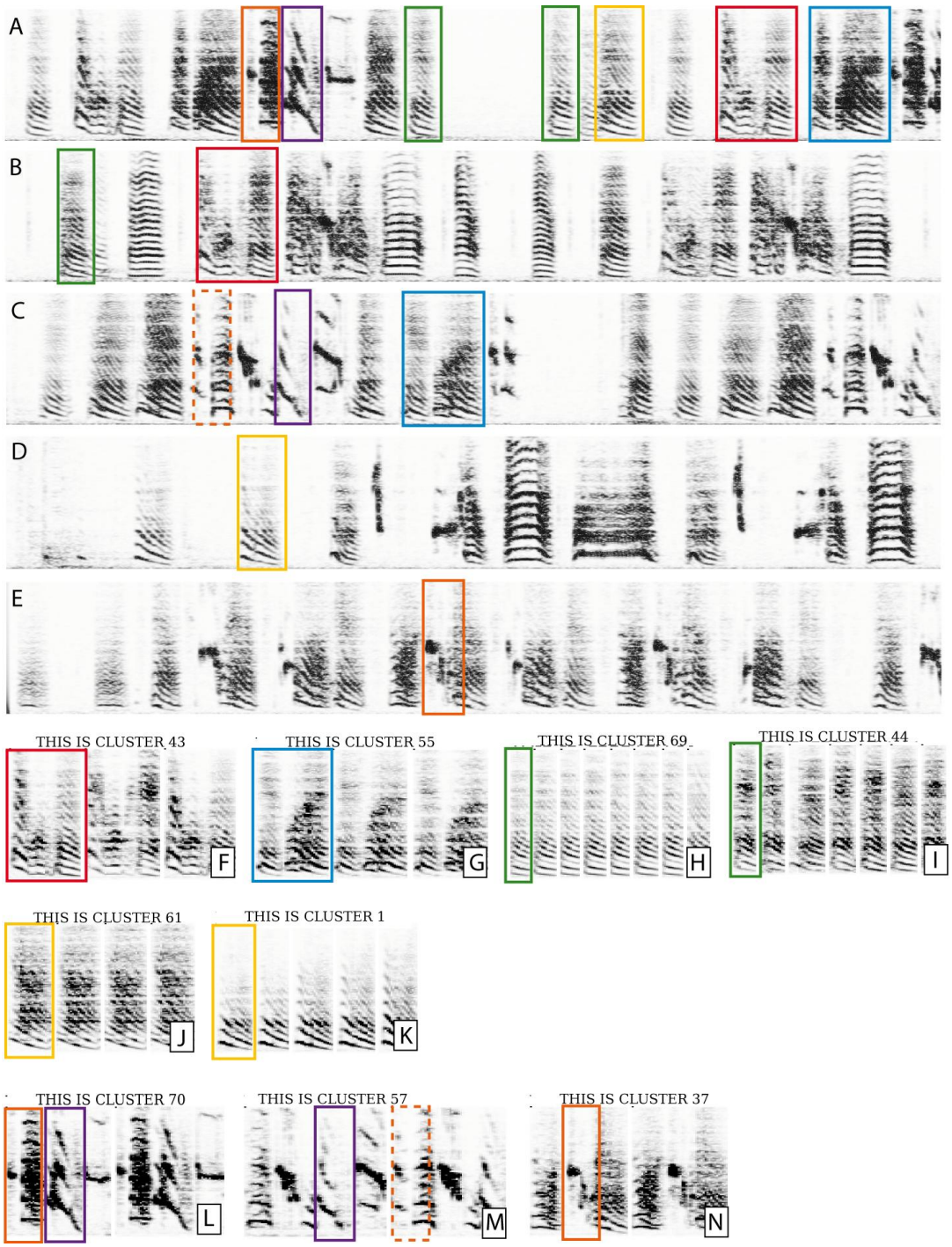

Figure 2.5: Example sonograms of song motifs and learned syllables from different categories in comparison to original motifs and syllables. This is also a nice example of a bird that learned from more than one tutor. Panel **A** shows the sonogram of the motif of a juvenile Zebra Finch (>100 days post hatching) from aviary 4. Panel **B**, **C**, **D** and **E** show sonograms of tutor 1 (main tutor), 2, 3 and 4 respectively. **F** and **G** show examples of category 1: copy. The juvenile shares these syllables with the tutor from whom they are learned (1 and 2 respectively). **H** and **I** show an example of category 2: imitation – H shows the offspring syllable, learned from I: the original tutor syllable (tutor 2). **J** and **K** show an example of category 3: variation – J shows the offspring syllable, learned from K: the original tutor syllable (tutor 3). **L**, **M** and **N** show an example of category 4: element – L shows the offspring syllable, learned from M (tutor 2) AND N (tutor 4). It is assumed that the element is learned from tutor 4 (orange lines), although it is also possible that it was learned from tutor 2 (dashed orange lines).

2.7.4 Tutor Identification

In order to investigate the origin of all offspring syllables that were not identified as real copies of tutor syllables, a stepwise procedure was followed for each aviary from experiment 1:

1) For all clusters, I printed at least 5 sonograms on paper and gave them to 10 independent observers. The observers compared the clusters that only contained offspring syllables with those containing tutor syllables. Then they were asked if the clusters of offspring syllables were learned from any of the clusters containing tutor syllables, or if they were unique. Observer scores were calculated for all possible combinations of offspring and tutor clusters.

2) For each clusters of offspring syllables the observers identified as learned from tutor syllables, 10 syllables were picked at random and compared to the tutor syllables. The similarity between offspring- and tutor syllables was then calculated with Sound Analysis Pro. Before I calculated between-cluster similarity scores, I looked at within-cluster similarity scores as controls. SAP similarity scores are based on various parameters (pitch; frequency modulation; amplitude; Wiener entropy; goodness of pitch) that are derived from the sound files. Sound Analysis Pro gives 3 similarity components (%similarity; accuracy; sequence) that can either be multiplied to get a product score, or can be used separately (SAP 1.2 User Manual). I used the first component for further analysis, which was the most relevant to us since we tested for similarity between single syllables instead of complete motifs (Maul *et al.* 2010). In case of the between-cluster comparisons, the % similarity represents the percentage of tutor's syllables included in offspring syllables (SAP 1.2 User Manual) and varies from 0 to 100%, with 100% being a perfect match.

3) Digital images of 5 random syllables per cluster were selected to calculate image overlap scores, which represent similarity in sonogram characteristics (greyscale). For all of the clusters of offspring syllables the observers identified as learned from a cluster of tutor syllables, automatic image comparisons were made between offspring cluster and tutor cluster. Within-cluster comparisons were made as controls, as well as comparisons between random clusters. The output of this analysis was an average difference in greyscale-value (0-255; 0 meaning perfect overlap) per pixel. This value was divided by 2.55 in order to get an overall image difference, which was then transformed into an image overlap score by subtracting the %difference from 100. The final score ranged from 0-100%, with 100% being a perfect match.

In experiment 2, tutor identification was based only on visual inspection of the clusters (Hanneke Poot and Andries ter Maat). Since tutor identification by visual inspection of the sonograms (step 1: observer scores) yielded good results in experiment 1, and because the number of potential tutors was lower, step 2 and 3 were not carried out here.

2.8 Analysis of Vocal Interactions (experiment 2)

For six complete days in February and March 2010 (11th, 18th and 25th of February and 05th, 11th and 18th of March), I analysed the recordings of all birds. The ages of the birds at these days are found in table 3.5.1. For each day, the sound files of all birds were cut into syllables AND calls. Noise (e.g. wing flapping) was discarded and the syllables and calls were clustered

with an automated K-means clustering paradigm for each bird individually, using Sound Explorer (June 2008).

At least 5 clusters of vocalisations (≥1 song syllable and ≥ 4 calls) were selected for each bird. Interactions between these clusters and any of the selected clusters of other birds were investigated. For vocalisations of each cluster, it was tested whether vocalisations of any other cluster, excluding those produced by the same bird, occurred significantly more often in the 2 sec. period before or after the vocalisation. The output of the analysis was a matrix with values indicating the strength of the interaction and a graphic representation with colour-coding for the strength of interactions. A script for automatic analysis was written in R 2.13.1 by Andries ter Maat.

For each bird, I investigated vocal interactions with all other birds. I looked with whom offspring interacted more: with other juveniles or with adults. Furthermore I studied the importance of family relations in vocal interactions. Most importantly, I explored whether there was a relationship between vocal interactions and learning. For this purpose, I tested whether offspring birds interacted more with the adult tutor from whom they learned (most of) their song than with others. Kruskal-Wallis One Way Analysis of Variance on Ranks and Dunn's Method all pairwise multiple comparison procedures were carried out to identify significant differences. SigmaPlot 11.0 and R 2.13.1 were used for all statistical analysis.

2.9 Statistics

I carried out most of the statistical analysis with SigmaPlot 11.0 and R 2.10.1 (R Development Core Team 2009). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.). Whenever different programs or versions were used, I specifically indicated this in the single sections of this chapter.

When testing for differences between density conditions, analyses were based on the number of aviaries rather than the number of animals in order to prevent pseudo-replication and in mixed effects models, density condition, aviary number and bird ID were included as random factors in the initial full models. Mixed effects models were used instead of repeated measures ANOVA because they can properly account for correlation between repeated measurements on the same subject, have greater flexibility to model time effects, and can handle missing data more appropriately. Proportion tests (prop.test: non-parametric 2-sample test for equality of proportions with continuity correction) were used to test for proportion differences between high- and low density aviaries. In proportion tests and one-way ANOVA, I pooled the data for both aviary 1 and 3 (high density) and 2 and 4 (low density). Parametric tests were only used when formal requirements were met and test statistics are provided in chapter 3.

Chapter 3

Results

3.1 Experiment 1A: Population Density

3.1.1 Breeding Success

No differences were found in nest building speed, laying date of the first egg, number of eggs per nest, and total number of hatchlings per nest (table 3.1.1). There was a tendency towards more offspring surviving until at least day 100 post hatching in low-density aviaries, but no significant difference was found (prop.test: χ^2=2.4885, df=1, p= 0.1147). Furthermore, the sex ratio of offspring surviving at least until 100 dph seemed female biased in low-density aviaries, but no significant differences were found here either (prop.test: χ^2=1.2664, df=1, p=0.2604).

Table 3.1.1. Total numbers of eggs, total number of chicks hatched, total number of chicks that survived until day 100 post hatching, and offspring sex ratio per aviary.

	aviary 1 (high)	aviary 3 (high)	aviary 2 (low)	aviary 4 (low)	total (high)	total (low)
total eggs laid	78	58	75	59	136	134
total eggs hatched	27	22	28	28	49	56
survived 100 dph	19	17	24	25	36	49
sex ratio (m:f)	11:8	9:8	10:14	10:15	1:0.8	1:1.45

3.1.2 Social Behaviour

In high density aviaries, more interactions were observed than in low-density aviaries. A significant difference (glm, binomial distribution, F=145.09, $p<2.2e^{-16}$) was found in the absolute numbers of social interactions (table 3.1.2). The proportions of aggressive vs. affiliate interactions differed significantly between high- and low density aviaries (prop.test: χ^2= 140.8865, df =1, $p< 2.2e^{-16}$), with relatively more aggressive interactions and less friendly interactions in high- than in low density aviaries.

Table 3.1.2. Social interactions per aviary and density-condition.

Aviary (density)	total interactions	aggressive interactions	affiliate interactions
1 (high)	542	310 (57%)	232 (43%)
3 (high)	496	222 (45%)	274 (55%)
mean (high)	519	266 (70%)	253 (43%)
2 (low)	441	103 (23%)	338 (77%)
4 (low)	465	122 (26%)	343 (74%)
mean (low)	453	112.5 (30%)	340.5 (57%)

3.1.3 Body Mass Adults

At the start of the experiment, no differences were found between the adult birds introduced to the experimental aviaries with respect to body mass and tarsus length. Also, no differences were found between males and females. Body mass distribution did not significantly differ from a normal distribution (shapiro.test: W=0.9734, p=0.09418). Although birds in all aviaries gained weight during the experiment, at the end of the experiment mean body mass was higher in low density aviaries (fig. 3.1.1A), but this was not significant (one-way ANOVA, df=1, residuals=61, F=2.1585, p=0.2938).

3.1.4 Body Sizes Offspring

At day 15, 60 and 100 post hatching, body mass of all offspring was measured. Tarsus length was only measured at day 15 and 60 because the bones are fully grown in the 7th week of development (Boruszewska *et al.* 2007). Mixed effects models (with temporal pseudo-replication) were calculated for tarsus length and body mass. Since gender and aviary number proved insignificant, these variables were removed from the models. As expected the offspring gained weight over time at about the same rate in both high- and low density aviaries. However, offspring in the low-density aviaries were consistently and significantly heavier (mixed effects model: effects of day post hatching and density condition on body mass; t=14,167, p<0.001, fig. 3.1.1B) than offspring in high-density aviaries, and had larger tarsus lengths (mixed effects model: effects of day post hatching and density condition on tarsus length; t=4.590, p=0.0195, fig. 3.1.1C).

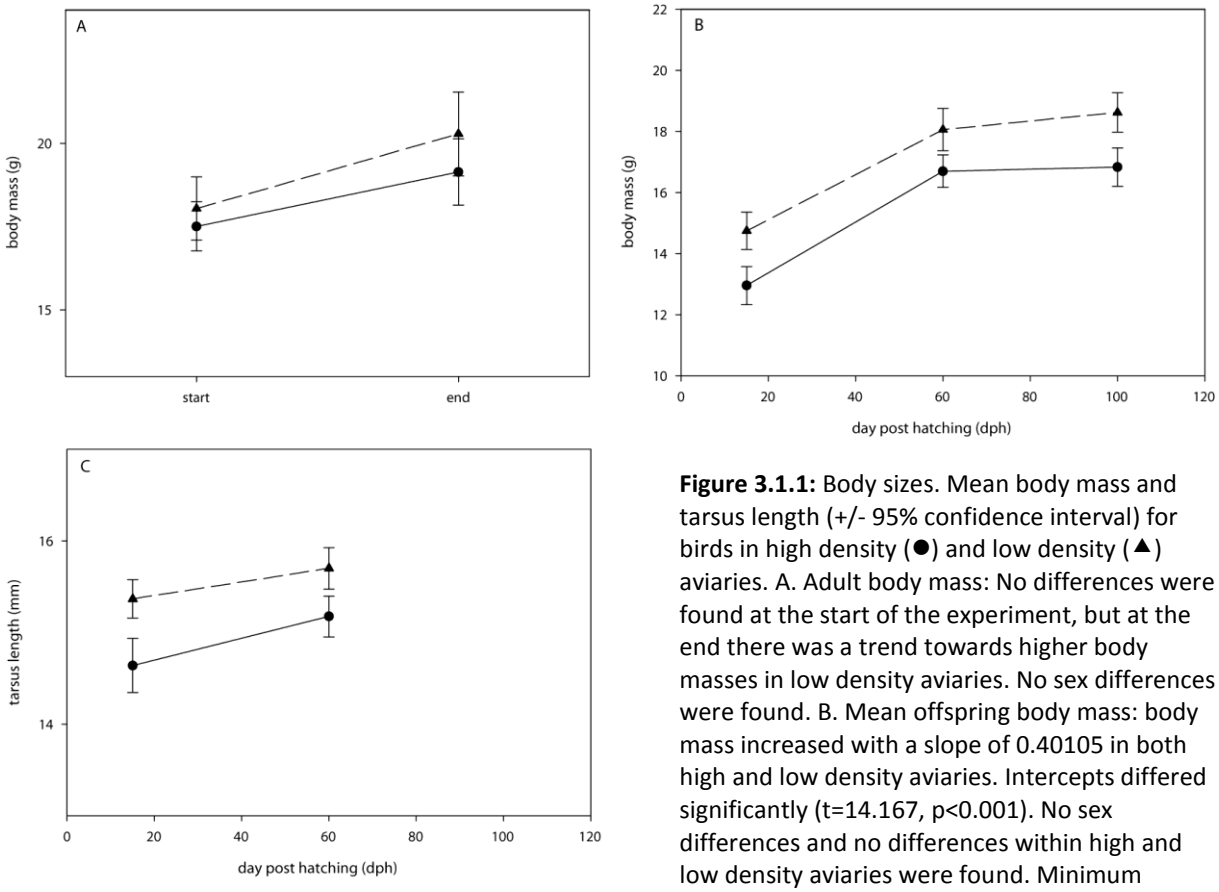

Figure 3.1.1: Body sizes. Mean body mass and tarsus length (+/- 95% confidence interval) for birds in high density (●) and low density (▲) aviaries. A. Adult body mass: No differences were found at the start of the experiment, but at the end there was a trend towards higher body masses in low density aviaries. No sex differences were found. B. Mean offspring body mass: body mass increased with a slope of 0.40105 in both high and low density aviaries. Intercepts differed significantly (t=14.167, p<0.001). No sex differences and no differences within high and low density aviaries were found. Minimum adequate model: lmer(mass~dph+density+(dph|birdID)+ (1|aviary)). C. Mean offspring tarsus length: tarsus length increased with a slope of 0.30353 in both high and low density aviaries. Intercepts differed significantly (t=4.590, p=0.0195). Minimum adequate model: lmer(tarsus~dph+ density+(dph|birdID)+(1|aviary)).

3.1.5 Song Complexity: Number of Syllables per Motif & Motif Duration

No differences were found in number of syllables per motif between adults and offspring in either high or low density aviaries (table 3.1.3. mixed effects model: effect of day post hatching (dph) and density condition on number of syllables per motif (aviary number = random effect) interaction age:density NS). However, male offspring seemed to produce a similar or lower total number of unique syllables in high density, and a higher total number of syllables in low density aviaries (table 3.1.3. mixed effects model: effects of day post

hatching (dph) and density condition on number of unique syllables (aviary number = random effect), interaction dph:density p=0.0498).

Table 3.1.3: Song complexity in adult and juvenile males per aviary. Mean motif duration per bird is calculated by taking the average of ten randomly picked motifs from all sound files produced in one day of recording and measured in ms. The overall average per aviary is presented here. Total number of syllables, number of syllables per motif and number of repeated syllables are counted from sonograms and averaged per aviary. A syllable is defined as "repeated syllable" when it occurs more than once in a motif.

aviary (density)	adult/ offspring	n	syllables p. motif	95% conf.	total syllables	95% conf.	repeated syllables	95% conf.	motif duration	95% conf.
1 (high)	adult	10	7.0	0.41	5.2	0.82	0.3	0.01	781.33	127.09
1 (high)	offspring	11	6.9	1.10	5.3	0.84	0.1	0.01	668.29	108.52
3 (high)	adult	10	7.8	1.40	5.6	0.93	0.7	0.02	1072.33	233.04
3 (high)	offspring	9	7.3	0.03	5.1	0.02	0.7	0.02	919.96	6.58
high	**adult**	20	**7.4**	0.02	**5.4**	0.02	**0.5**	0.01	**926.83**	4.63
high	**offspring**	20	**7.1**	0.02	**5.2**	0.02	**0.4**	0.01	**781.54**	3.86
2 (low)	adult	10	10.0	0.03	5.1	0.03	0.5	0.02	868.75	5.19
2 (low)	offspring	10	7.8	0.04	6.0	0.03	0.9	0.02	974.77	4.36
4 (low)	adult	10	9.1	0.05	5.1	0.03	0.2	0.01	853.53	4.05
4 (low)	offspring	10	10.7	0.05	6.2	0.02	0.5	0.02	946.99	3.54
low	**adult**	20	**9.6**	0.03	**5.1**	0.02	**0.4**	0.01	**861.14**	3.21
low	**offspring**	20	**9.3**	0.04	**6.1**	0.02	**0.7**	0.01	**960.88**	2.74

A similar but stronger difference was found for mean motif duration (fig. 3.1.2): male offspring in high density aviaries produced shorter motifs than their tutors, whereas offspring in low density aviaries produced longer motifs (table 3.1.3. mixed effects model: effects of day post hatching (dph) and density condition on log. motif duration (aviary number = random effect) interaction dph:density p=0.0237).

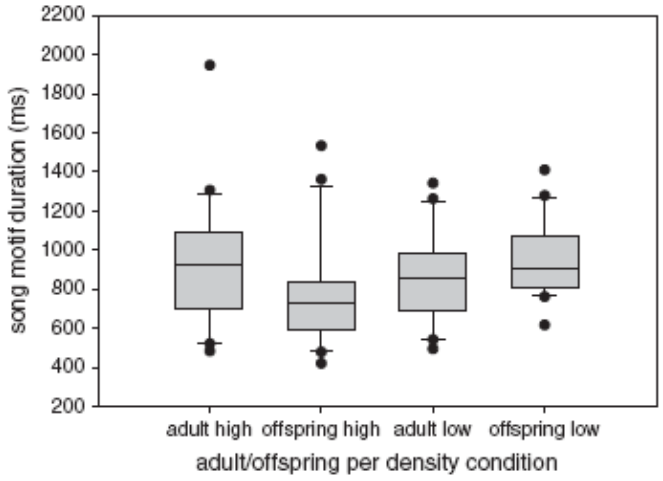

Figure 3.1.2: Song Motif Duration
Mean song motif duration (ms) for adults and offspring per density condition. A significant interaction was found between age (adult/offspring) and density condition. Full model: Lme (duration~age* density,random=~1| aviary).

3.1.6 Corticosterone Levels Adults

In the samples taken at the start of the experiment (hereafter called 'before'-samples), baseline corticosterone levels seemed higher in high density aviaries (fig. 3.1.3A) but no significant differences were found (mixed effects model: effects of time (before/after) and density condition on plasma corticosterone level, random effects: bird ID and aviary number). At the end of the experiment, levels did not differ between high and low density

aviaries. Furthermore, baseline corticosterone levels in samples taken at the start and at the end of the experiment all lay in the same range (fig. 3.1.3A).

3.1.7 Corticosterone Levels Offspring

Blood samples were also taken from all offspring at days 15, 60 and 100 post hatching. They were treated the same way as the samples described previously. Statistical analysis (mixed effects model: effects of day post hatching (dph) and density condition on plasma corticosterone level, random effects: bird ID and aviary number)) showed that corticosterone concentrations varied significantly between day 15, when the juveniles are still in the nest but almost ready to fledge, and days 60 and 100 ($t = -7.558190$, $df = 162$, $P<0.001$). This pattern was found in all aviaries irrespective of density (fig. 3.1.3B).

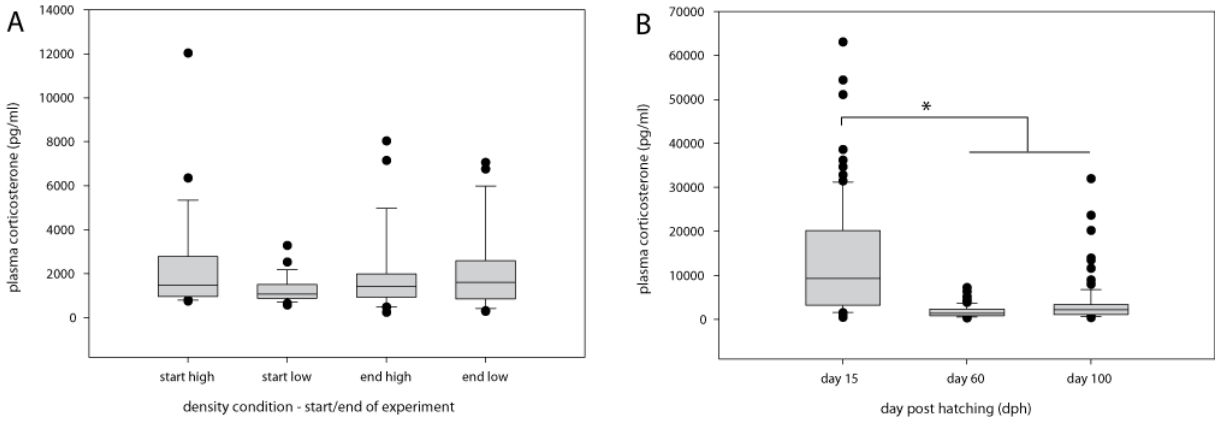

Figure 3.1.3: Mean baseline plasma corticosterone levels (pg/ml) per density condition.
A. Adult birds at the start and at the end of the experiment. No significant differences were found, levels lie in the same range for all conditions. B. Offspring at day 15, 60 and 100 post hatching. Since no differences were found between density conditions, data of all birds were added together.

3.1.8 Effects of Brood Size

Based on the distribution found in the study population, nests were divided into 3 brood size categories: small (1, 2 chicks: n= 12); medium (3 chicks; n=10); and large (4, 5, 6 chicks; n=9). Possible effects of brood size on offspring plasma corticosterone, body mass and tarsus length (measured at day 15, 60 and 100 post hatching) were investigated using mixed effects models (effect of brood size, density condition, day post hatching (dph) and possible interaction terms on corticosterone, mass and tarsus were tested respectively, random effects: aviary number, nest number, bird ID).

For plasma corticosterone, “day post hatching” proved to be significant ($p<0.001$; as described in section 3.1.7), and a significant interaction was found between “day post hatching” and “brood size” ($p=0.0275$), but not between “brood size” and “density” (fig. 3.1.4A). On day 15 post hatching, plasma corticosterone levels were higher in medium and large broods than in small broods. For body mass and tarsus length, mixed effects models did not reveal any significant effect of brood size (fig. 3.1.4B, C.).

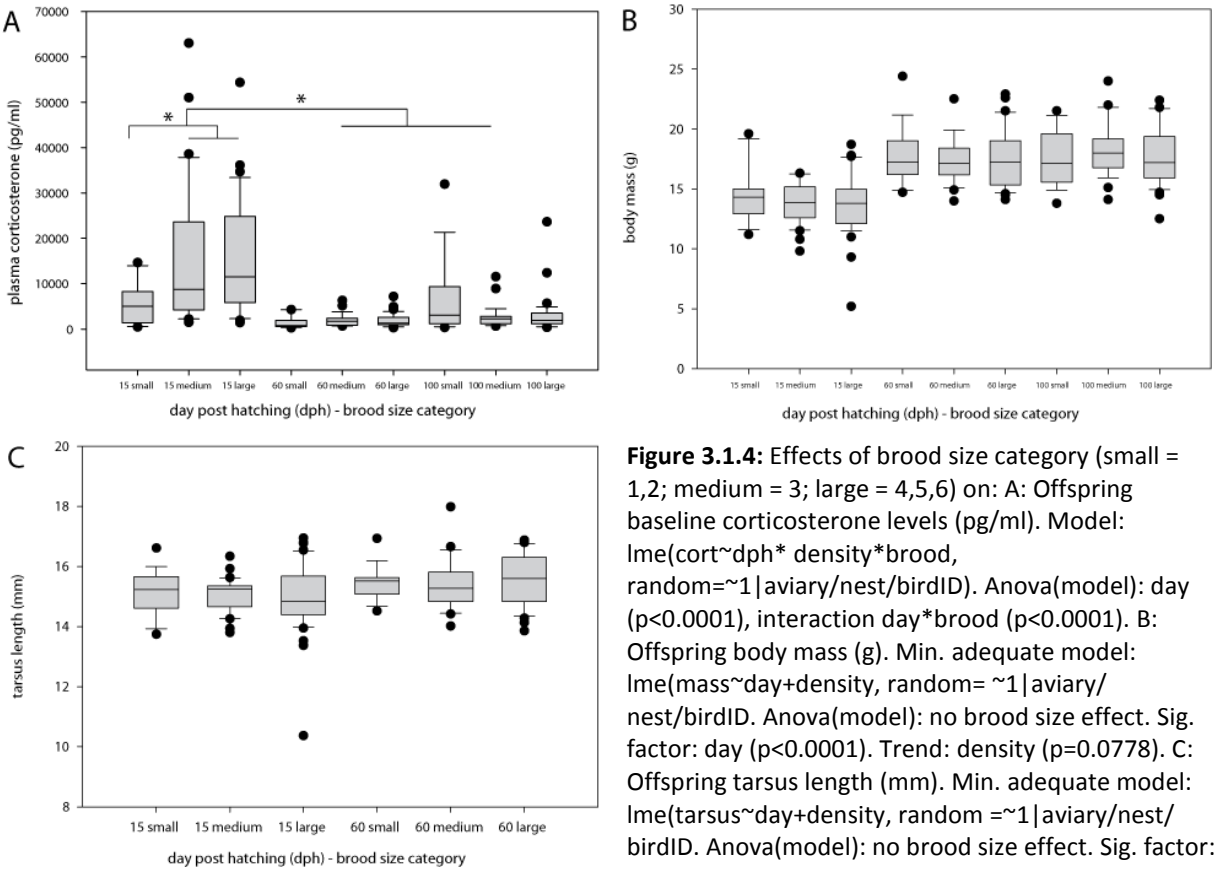

Figure 3.1.4: Effects of brood size category (small = 1,2; medium = 3; large = 4,5,6) on: A: Offspring baseline corticosterone levels (pg/ml). Model: lme(cort~dph* density*brood, random=~1|aviary/nest/birdID). Anova(model): day ($p<0.0001$), interaction day*brood ($p<0.0001$). B: Offspring body mass (g). Min. adequate model: lme(mass~day+density, random= ~1|aviary/ nest/birdID. Anova(model): no brood size effect. Sig. factor: day ($p<0.0001$). Trend: density ($p=0.0778$). C: Offspring tarsus length (mm). Min. adequate model: lme(tarsus~day+density, random =~1|aviary/nest/ birdID. Anova(model): no brood size effect. Sig. factor:

3.2 Experiment 1B: Social Dominance

3.2.1 Dominance Patterns

Based on agonistic behaviour, clear dominance patterns could be observed in all aviaries: some animals were consistently more dominant than others and no indications were found for either males or females being more dominant. The dominance structures were not strictly linear (low values of h, h' and K: N.S.) because of the relative high numbers of inconsistencies (indicating triangular dominance relationships, (De Vries 1998; De Vries 1993), but hierarchies could be identified nonetheless (table 3.2.1). DCI was high for all aviaries, indicating uni-directionality within the hierarchies.

Data of all 40 males and 40 females from the four aviaries were added together and density condition and aviary number were used as random effects in statistical analysis (mixed effects models). Behaviour ranks were correlated to average perching position, physiological traits and reproductive success for all individuals.

3.2.2 Correlations between Dominance and Physiological & Behavioural Traits

Body mass (at the start of the experiment) and tarsus length were positively correlated, indicating that heavier birds are bigger in all aviaries (lme $p< 0.001$: table 3.2.2). Body mass was chosen as a measure of body size for further analysis. A positive correlation was also found between number of syllables per motif and motif duration, indicating that motifs with more syllables have a longer duration in all aviaries, although variation was also found between aviaries (lme $p<0.001$, random effect 'aviary' explains 11% of variance: table 3.2.2).

Table 3.2.1: Quantitative description of dominance hierarchy for each experimental aviary. DCI (Directional Consistency Index) ranges from 0 (complete equal exchange) to 1 (complete uni-directionality). h (Landau's linearity index) and h' (Landau's linearity index, corrected for unknown relationships) and K (Kendall's coefficient of linearity) range from 0 (absence of linearity) to 1 (complete linearity). From $\chi 2$ and df (degrees of freedom, a p-value was calculated, with $p<0.05$ indicating a significantly linear dominance hierarchy.

Linear Hierarchy	**aviary 1 (small)**	**aviary 3 (small)**	**aviary 2 (large)**	**aviary 4 (large)**
total aggressive interactions	310	222	103	122
DCI (Directional Consistency Index)	**0.78**	**0.77**	**0.81**	**0.80**
h (Landau's linearity index)	0.16	0.20	0.04	0.07
h' (corrected for unknown relationships)	0.22	0.26	0.22	0.17
K (Kendall's coefficient of linearity)	0.16	0.20	0.01	0.06
$\chi 2$ (df)	30 (27)	37 (27)	20 (27)	14(27)
p	0.314	0.095	0.997	0.981

Table 3.2.2: Overview of all calculated mixed effects models with random effects 'density' (high or low) and 'aviary' (1,2,3,4) and standard deviation and % of variance that could be explained by each random factor. Furthermore, the total degrees of freedom (DF), t-value for both intercept and interaction for each model are given, as well as the correlation coefficient. Group size for most analyses was 80 (40 males and 40 females). For analyses concerning song parameters, group size was 40 (all males) and for the model with baseline corticosterone levels, group size was 48 (all sampled animals).

linear mixed effects	random eff. density		random eff. aviary		(intercept)			perching			correlation
model (lme)	SD	% var	SD	% var	DF	t-value	p-value	DF	t-value	p-value	
lme(mass~tarsus, random=~1|density/aviary)	$7.17e^{-05}$	$1.11e^{-07}$	$8.66e^{-06}$	$1.39e^{-09}$	75	-0.51259	0.6097	75	5.03858	**0.0000**	-0.998
lme(syllables~duration, random=~1|density/aviary)	$3.68e^{-05}$	$1.58e^{-07}$	0.30612	10.8798	35	3.35808	0.0019	35	7.80796	**0.0000**	-0.914
lme(mass~syllables, random=~1|density/aviary)	0.00013	$2.65e^{-07}$	$3.18e^{-06}$	$1.62e^{-10}$	35	12.9356	0.0000	35	-1.72118	*0.094*	-0.968
lme(mass~duration, random=~1|density/aviary)	0.00013	$2.90e^{-07}$	$1.38e^{-05}$	$3.12e^{-09}$	35	15.4309	0.0000	35	-2.01636	*0.0515*	-0.955
lme(behaviour~perching, random=~1|density/aviary)	0.00024	$1.74e^{-07}$	$2.87e^{-05}$	$2.59e^{-09}$	75	5.96217	0.0000	75	2.32299	**0.0229**	-0.877
lme(behaviour~mass, random=~1|dens/av)	0.00246	$1.92e^{-07}$	$2.88e^{-05}$	$2.64e^{-09}$	75	4.93937	0.0000	75	-2.51301	**0.0141**	-0.989
lme(behaviour~cort, random=~1|density/aviary)	0.00025	$1.79e^{-07}$	$2.83e^{-05}$	$2.32e^{-09}$	43	8.9007	0.0000	43	0.13896	0.8901	-0.698
lme(behavaiour~offspring, random=~1|density/aviary)	0.00024	$1.78e^{-07}$	$2.96e^{-05}$	$2.59e^{-09}$	75	12.2926	0.0000	75	-0.83407	0.4069	-0.688
lme(behaviour~syllables), random=~1|density/aviary)	1.11443	3.61716	0.00023	$1.49e^{-07}$	35	1.6812	0.1016	35	1.06606	0.2937	-0.946
lme(behaviour~duration), random=~1|density/aviary)	1.06726	3.30806	0.00024	$1.67e^{-07}$	35	2.25789	0.0303	35	0.96585	0.3407	-0.927

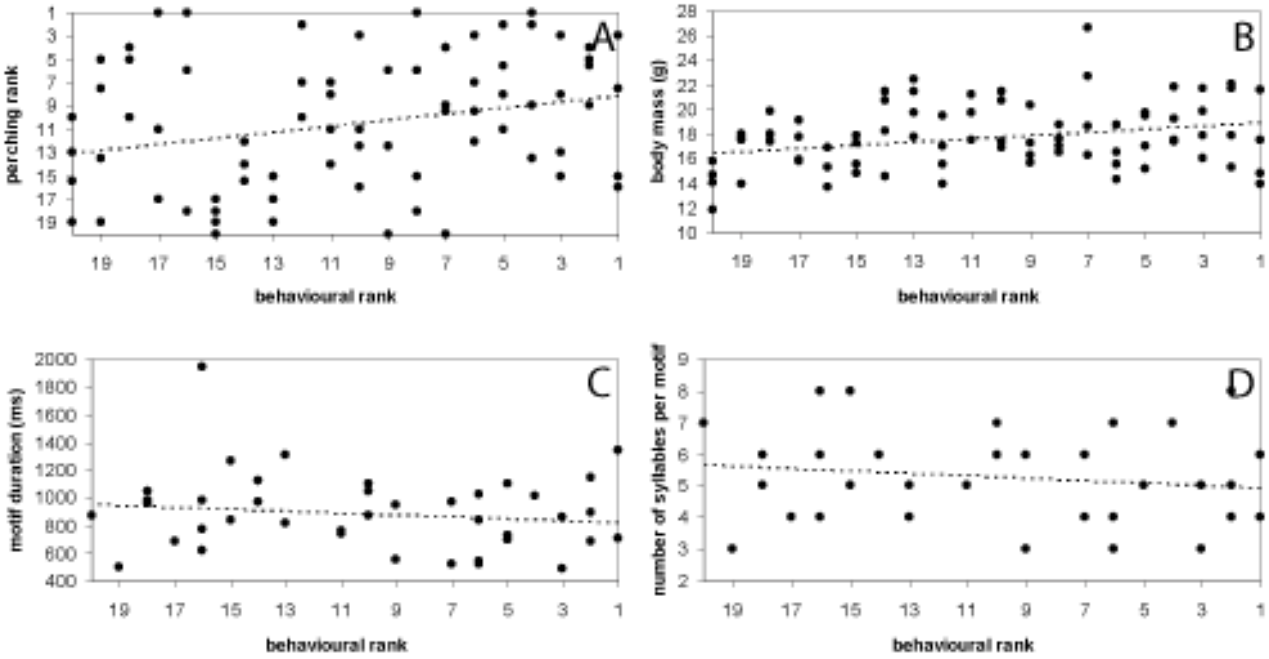

Figure 3.2.1: Behavioural rank is significantly correlated to (A) perching rank and (B) body mass. No correlation was found between behavioural rank and (C) motif duration and (D) number of syllables per motif.

Behavioural rank was weakly but significantly correlated to perching rank (lme p=0.0229: fig. 3.2.1A, table 3.2.2), with more dominant birds occupying higher perches. Behavioural rank was also correlated to body mass (lme p=0.0141: fig. 3.2.1B, table 3.2.2), indicating that bigger birds are generally more dominant.

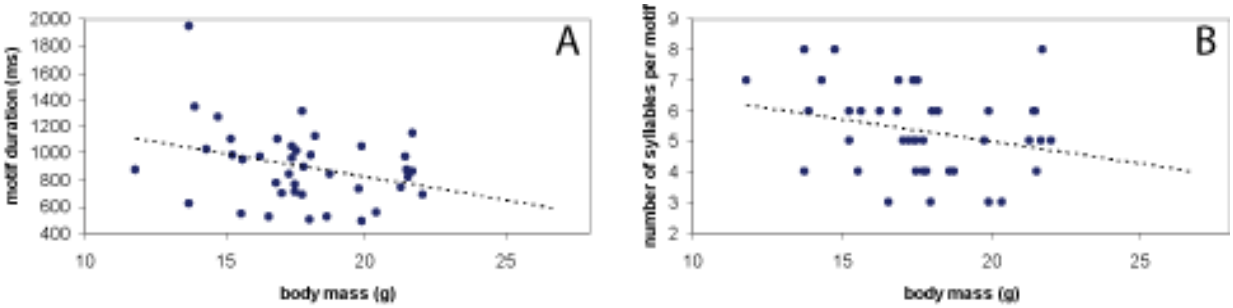

Figure 3.2.2: Body mass (indicator for body size) correlated to (A) motif duration and (B) number of syllables per motif. A trend was found towards lower song complexity in bigger birds.

No clear correlations were found between behavioural rank and baseline corticosterone levels (lme p=0.8901: fig. 3.2.3A, table 3.2.2) and there was no evidence that behavioural rank was correlated with reproductive success, as defined as number of offspring (lme p=0.4069: fig. 3.2.3B, table 3.2.2).

Statistical analysis revealed a trend towards lower numbers of syllables per motif and shorter motif duration respectively in birds with higher body mass (lme p= 0.094 and p=0.0515 respectively: table 3.2.2), as shown in fig. 3.2.2A and B. This indicates that bigger birds would produce less complex song. However neither number of syllables per motif, nor motif duration was correlated to behavioural rank (lme p= 0.2937 and p=0.3407 respectively: fig. 3.2.1C and 3.2.1D, table 3.2.2).

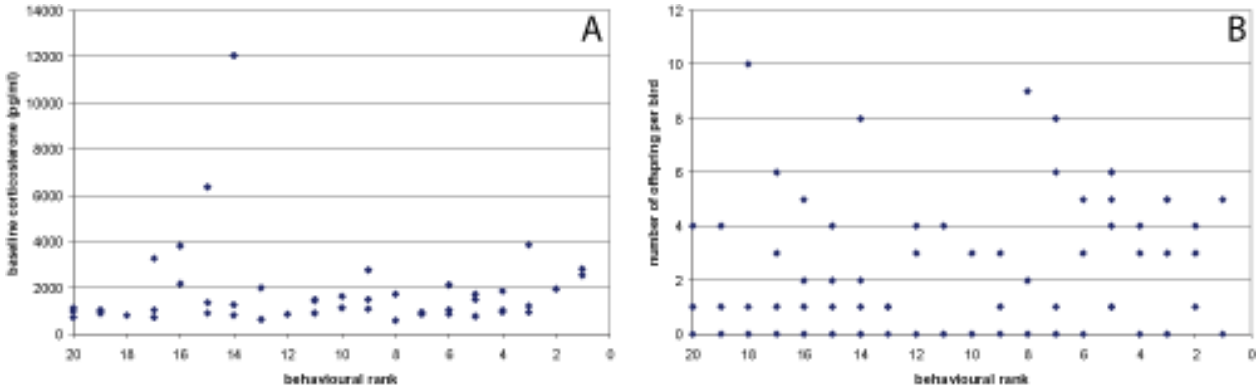

Figure 3.2.3: Behavioural rank plotted against (A) baseline corticosterone levels; (B) number of offspring per bird (= reproductive success). No statistically significant correlations were found.

3.3 Experiment 1C: Behavioural and Reproductive Patterns

3.3.1 Pair Dynamics

Five birds had more than one partner during the experiment (table 3.3.1), sometimes even at the same time. Most nest boxes were defended and cared for by a pair, but 3 of the 40 boxes were defended by females only, and one box was only defended by a male. 2 of these female nests did not produce any offspring, but the clutch in the third box was sired by multiple fathers. In the male nest, only one chick hatched. In one aviary a female homosexual pair was observed, who also defended a nest box. The overall rate of extra-pair offspring (EPO) was 16.5% and one case (1.2%) of intra-specific brood parasitism was found.

Table 3.3.1: Pair dynamics, successful extra-pair copulations (EPC) and extra-pair offspring (EPO) per aviary. Only offspring that survived until at least day 100 post hatching were included in this analysis. Birds engaged in successful extra-pair copulations are defined as birds that are involved in a pair bond AND produce offspring with another bird outside of the pair bond. In aviary 1 and 2, where there were females that engaged in EPC but no males, the females had offspring with single males.

	aviary 1	aviary 2	aviary 3	aviary 4
paired females	6	9	8	9
paired males	6	8	8	7
females >1 partner	0	1	1	0
males > 1 partner	0	2	1	0
homosexual pairs	0	0	0	1
pair nests	9	9	8	9
female nests	1	0	1	1
male nests	0	1	0	0
brood parasitism	0	0	0	1
females engaged in successful EPC	1	4	1	2
males engaged in successful EPC	0	0	1	1
total number of EPO (offspring)	3	5	2	4
total within pair offspring	16	19	15	21

3.3.2 Reproduction & Behaviour

Individual differences in reproductive and behaviour patterns were observed in all four aviaries. Five categories could be defined: 1) monogamous pair *with* offspring, *without* EPO; 2) monogamous pair *with* offspring, *with* EPO; 3) monogamous pair *without* offspring; 4) single *with* EPO; 5) single *without* offspring. Categories 1, 2, 3 and 5 were represented in all experimental aviaries and category 4 was only found in aviary 1 and 2 (table 3.3.2).

Table 3.3.2: Numbers of individual birds (male and female) per category per aviary, with a total of 20 birds per aviary. Categories: 1) monogamous pair with offspring, without EPO; 2) monogamous pair with offspring, with EPO; 3) monogamous pair without offspring; 4) single with EPO; 5) single without offspring. The distributions over the categories did not differ between the aviaries (Fisher's Exact Test for Count Data p=0.3936).

category	aviary 1 (high)	aviary 2 (low)	aviary 3 (high)	aviary 4 (low)
1	6	7	10	11
2	3	6	3	3
3	3	4	4	2
4	1	2	0	0
5	7	1	3	4

Despite this small inconsistency, no differences in general distribution of these categories were found between the 4 experimental aviaries (Fisher's Exact Test for Count Data p=0.3936) and therefore the data of all aviaries were added together for further analysis. The general distribution over all categories found in the aviaries was different from an equal distribution (Fisher's Exact Test for Count Data p=0.0027), in favour of categories with offspring. No gender differences were found in distribution over the categories (Fisher's Exact Test for Count Data p=0.8647): Males and females seemed to follow the same strategies to the same extent (fig. 3.3.1).

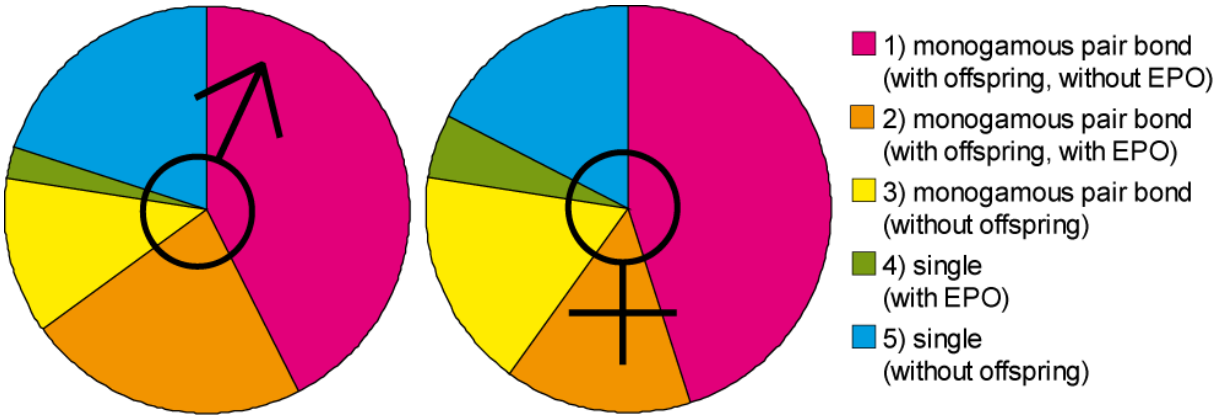

Figure 3.3.1: Reproductive- and behaviour patterns per gender (females: n=40; males: n=40). No differences were found (Fisher's Exact Test for Count Data p=0.8647).

3.3.3 Reproductive Success

Differences in reproductive success (expressed as number of offspring per bird) were found between the different categories described above (fig. 3.3.2.), which proved to be statistically significant (ANOVA, p=0.0062, df 2). A general linear model with poisson errors was used to test for statistical differences in number of offspring between reproductive strategies. Birds in category 2 produced more offspring per bird than those in category 1, although statistically this was only a trend (p=0.0686). Paired birds (category 1 and 2)

produced significantly more offspring than single birds with EPO (category 3; p=0.0108 and p=0.0011 respectively).

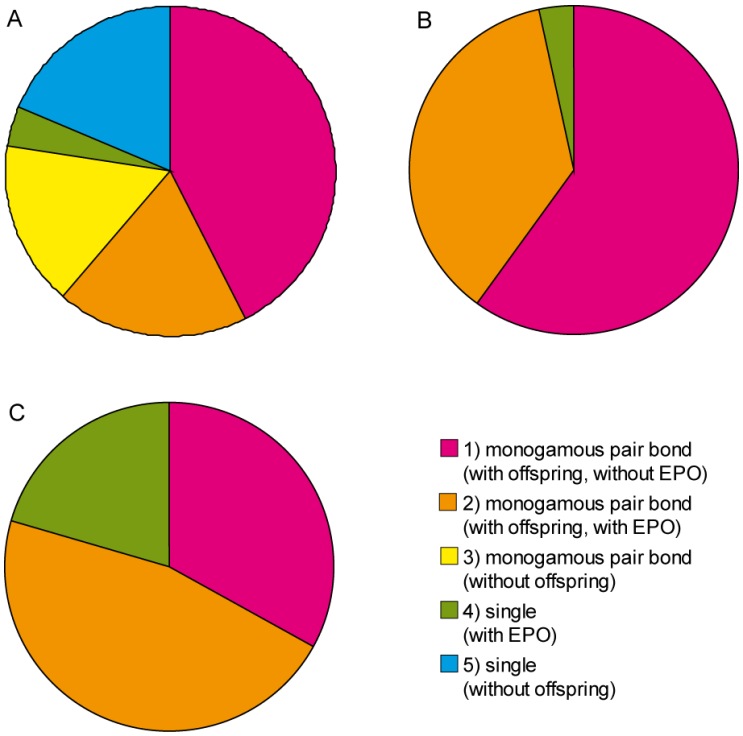

Figure 3.3.2: Overview of reproductive- and behaviour patterns (category 1-5) found in all 4 aviaries (80 individuals, male and female) and corresponding reproductive success. A: absolute proportion of birds following different reproductive/behaviour patterns (category 1-5) for all aviaries; B: absolute proportion of total offspring per category (1-5) for all aviaries; C: absolute proportion of offspring per bird per category (1-5), corrected for overall differences in absolute frequencies of strategies.

3.4 Experiment 1D: Song Learning and Tutor Choice

3.4.1 Clustering

Automatic clustering of all syllables produced per aviary resulted in 70-80 unique clusters of song syllables per aviary (calls were discarded), which were either produced by tutors, offspring, or tutors and offspring (i.e. offspring produced real copies of tutor syllables).

As shown in fig. 2.4 and 2.5, offspring syllables were classified as: (1) real copies of tutor syllables; (2) imitations of tutor syllables; (3) variations on tutor syllables; (4) elements of tutor syllables; or (5) new syllables. Syllables from category 1-4 were clearly learned, whereas for category 5 it was unclear where they originated from. From here on, the term "learned syllables" will be used as a hypernym for syllables from categories 1-4.

Observer scores were only calculated for category 2-4, since observers did not score real copies (they emerged from the automatic clustering procedure). Figure 3.4.1 shows the range of, and differences between syllable categories for observer scores, SAP-scores and image-overlap-scores. For observer scores, significant differences were found between imitation and variation, imitation and element, and variation and element (one-way ANOVA $p<0.001$, Holm-Sidak post-hoc test: $p<0.001$, $p=0.012$ and $p=0.011$ respectively). A Kruskal-Wallis one-way analysis of variance on ranks ($H=253.022$ on 4DF, $p<0.001$) with subsequent Dunn's pairwise comparisons (post-hoc test) revealed that the %similarity scores calculated with Sound Analysis Pro differed significantly between category 1 (copy) and all other categories, but differences among these other categories and random comparisons (control)

were not as clear. However, category 2, 3 and 4 together did differ significantly from random comparisons (H=5.150, DF=1, p=0.023). A similar result was found with the image overlap scores: a Kruskal-Wallis one-way analysis of variance on ranks yielded H=51.914 on 4DF and p<0.001. Dunn's pairwise comparisons were significant for category 1 versus all other categories and a trend was found towards a difference between category 2, 3 and 4 (together) and random comparisons (H=3.403, DF=1, p=0.065).

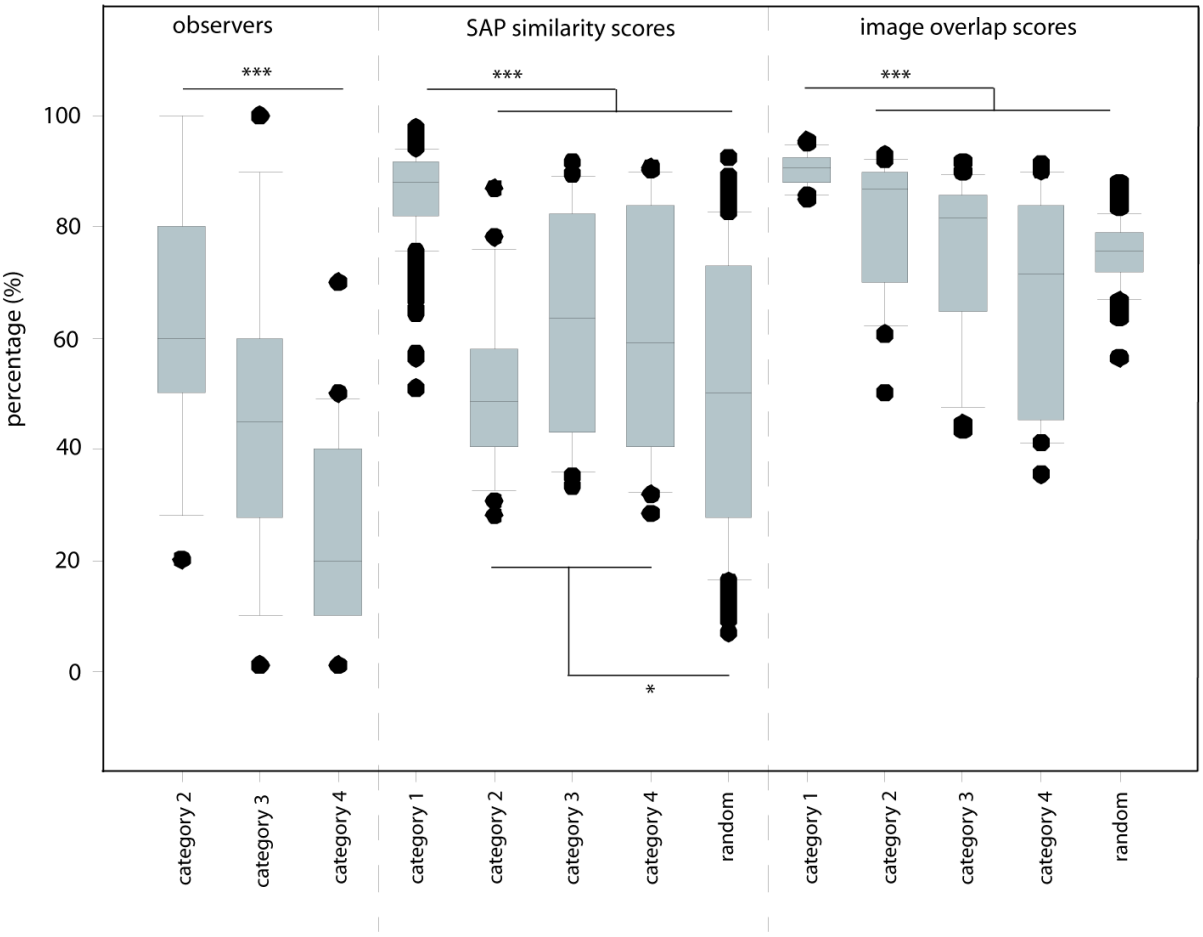

Figure 3.4.1: Percentage scores for comparison between tutor- and offspring syllable clusters of the different categories. A score of 100% means a perfect match. Observers: score for visual inspection by 10 independent observers. SAP: similarity scores (Sound Analysis Pro) for within cluster comparison (copy) and between cluster comparisons and random comparison as controls. Image overlap scores for within cluster comparison (copy) and between cluster comparisons and random comparison as controls. Category 1: copy; category 2: imitation; category 3: variation; category 4: element.

All syllable categories (1-5) were found in all experimental aviaries (fig. 3.4.2), but the actual distribution of syllables produced by the offspring differed between the aviaries (Pearson's χ^2 Test: χ^2=28.9083, df = 12, p = 0.0041).

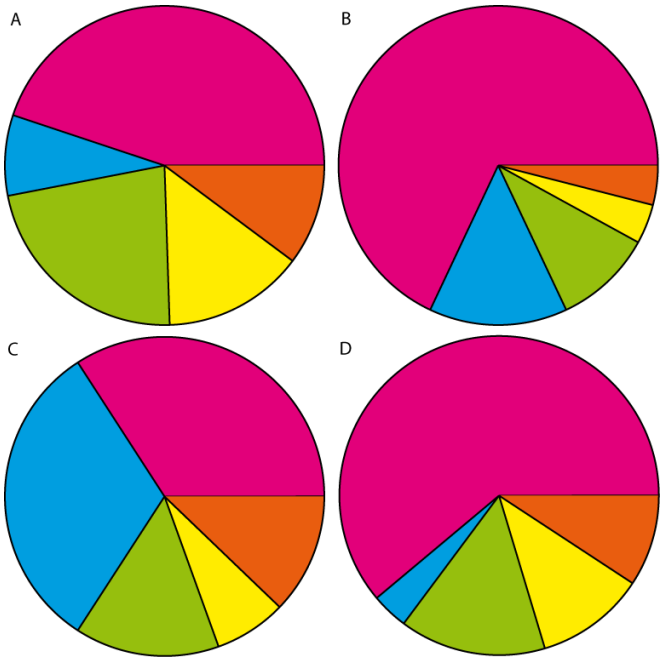

Figure 3.4.2: Distribution of all syllables produced per aviary, divided over the different categories

- copy;
- imitation;
- variation;
- element;
- new.

A: aviary 1, n = 49 syllables
B: aviary 2, n = 50 syllables
C: aviary 3, n = 41 syllables
D: aviary 4, n = 54 syllables

3.4.2 Tutor Preferences

In all experimental aviaries, offspring males learned noticeably more from certain tutors than from others (fig. 3.4.3), indicating a tutor preference. Since the patterns of tutor preference were similar in all aviaries, data were added together for statistical analysis.

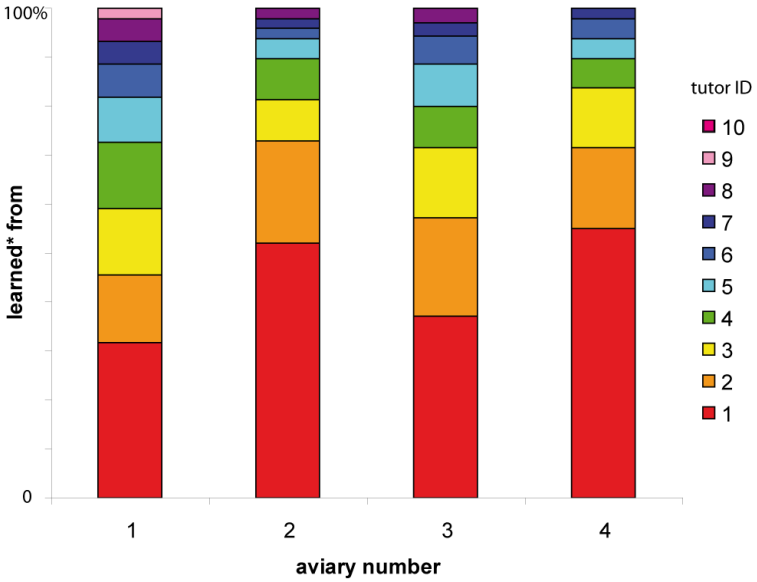

Figure 3.4.3: Percentage of offspring syllables that were learned from the adult tutors (1-10) present in each aviary. The designated colours for each tutor are also used in the following figures.

Aviary 1: DG-W; DB-HB; G-S; P-S; ST-ST2; DG-G; DG-S; L-T2; R-W; HB-O
Aviary 2: DG-DG; HB-T; DG-HB; HG-L; G-W; DG-HG; DG-T; R-S; DB-G; T-W
Aviary 3: HB-L; DB-L; S-T; DB-O2; DB-W; HG-W; DB-T; ST-W; DB-S; S-S
Aviary 4: DB-DB; L-S2; DG-L; W-W; DB-DG; HB-HB; HB-W; G-HG; HG-S; P-W

Observed and expected frequencies (binomial distribution) of tutor choice were calculated for category 1 (copy) for each aviary. Category 1 (copy) was chosen for analysis since it is most frequent and representative for the other learning categories. Data were divided into classes: adults that were never chosen (0), adults that were chosen by one or two offspring (1, 2), and adults that were chosen by three or more offspring (≥ 3), and a chi-square test

was carried out (table 3.4.1). The results of this test confirm that tutor choice is not random, which again indicates that offspring birds prefer certain adults over others as song tutors.

Table 3.4.1: test statistics for tutor choice. Data for all aviaries are combined and category 1 (copy) is tested, as representative for all learning categories. The observed values differ significantly from the expected values (binomial distribution), indicating significant tutor preferences.

Class	Expected	Observed	Chi-squared
0	13.57	20	3.04678703
1,2	22.689	12	5.03568782
≥ 3	2.284	7	9.73759019
df (degrees of freedom)			2
Chi-squared			17.820065
p-value			0.00013503

In order to find out whether the preferred tutors were genetically or socially related to the offspring, diagrams as shown in fig. 3.4.4 for category 1 (copy) in aviary 2 were created for all learning categories in all aviaries (appendix). Aviary 2 was picked as an example and is representative for all aviaries (table 3.4.2). The sonograms of the motifs of all males (adults and offspring) from aviary 2 are presented in fig. 3.4.6.

In aviary 2 the offspring males did not learn more from their fathers (genetic and/or social) than from other adult tutors. Similar patterns were found in all aviaries: preferred tutors were not necessarily related (genetically and/or socially) to the offspring males. Syllable sharing was common among peers (fig. 3.4.5) and tutor preference seemed consistent.

Table 3.4.2: Percentage of syllables learned from the father (genetic + social) and other tutors. N= number of learned syllables.

	father	other	n
aviary 1	4.55%	95.45%	44
aviary 2	33.33%	66.66%	48
aviary 3	34.29%	65.71%	35
aviary 4	22.45%	77.55%	49

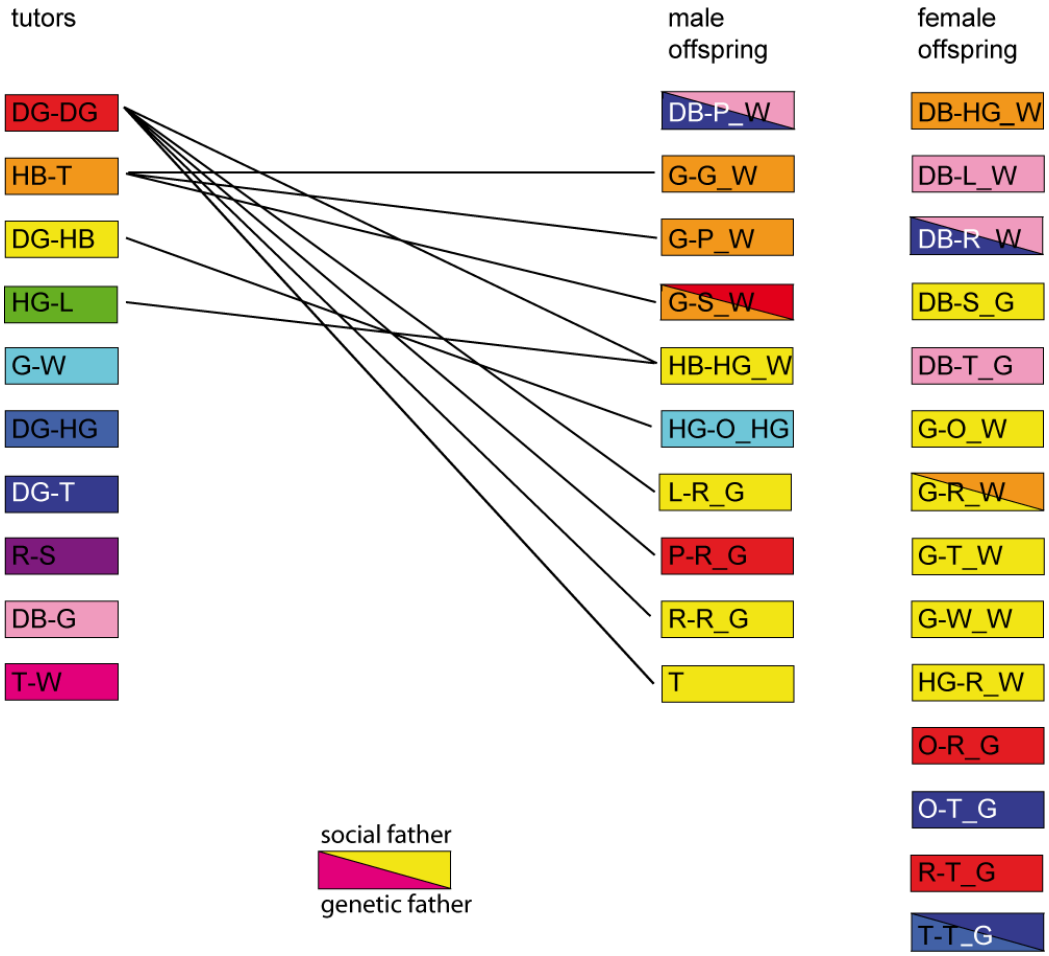

Figure 3.4.4: Syllable learning (category 1: copy) in aviary 2. Same colours represent family relations: in case of extra-pair offspring, both genetic and social father are indicated. Lines between offspring and tutors indicate that the offspring bird has learned at least one syllable from the tutor to whom he is connected.

aviary 2	DB-P_W	G-G_W	G-P_W	G-S_W	P-R_G	HB-HG_W	L-R_G	R-R_G	T	HG-O_HG
DB-P_W										
G-G_W			2	2						
G-P_W		2		3						
G-S_W		2	3							
P-R_G							5	3	4	
HB-HG_W							1			
L-R_G					5	1		4	4	
R-R_G					4		4		3	
T					4		4	3		
HG-O_HG										

Figure 3.4.5: Syllable sharing among siblings. Same colours represent family relations: in case of extra-pair offspring, both genetic and social father are indicated. Similar figures were created for all aviaries and are found in the appendix.

Table 3.4.3 gives an overview of tutor characteristics measured in part A-D for aviary 2, which is representative for all aviaries (data for other aviaries are found in the appendix). It was shown that the total number of syllables that was learned from a tutor (category 1-4) was not correlated to pair status (paired to a female or single: p=0.7684), total number of offspring (p=0.2457), number of extra-pair offspring (p=0.5142), dominance rank based on behaviour (p=0.2483), or body mass (p=0.4928). For statistical analysis, mixed effects models (lme(syllables ~*factor*, random= ~1|density/aviary), DF = 35) were calculated in R

2.10.1 (R Development CoreTeam 2009). Possible effects of song characteristics (syllables per motif; motif duration; SAP similarity score) were only calculated for aviary 2 (Spearman rank tests p=0.7266; p=0.5724 and p=0.6703 respectively), but no significant effects were found here either.

Table 3.4.3: Characterisation of all adult males (tutors) in aviary 2, which is representative for all aviaries. Percentage of all learned offspring syllables that could be attributed to this tutor; was the male paired to a female (yes/no); total number of offspring that survived at least until day 100 post hatching; number of extra-pair offspring (EPO) from total number of offspring; social rank, based on agonistic interactions, with rank 1 = most dominant male; body mass at begin of experiment in gram; number of syllables per motif; motif duration in ms; SAP similarity-score (indication for motif consistency). This table presents a synthesis of data from part A-D.

tutor	learned	paired	offspring	EPO	rank	mass	syll/motif	duration	similarity
DB-G	0.0%	yes	2	0	7	15.27	6	982.325	61.85
DG-DG	52.1%	yes	4	1	2	21.7	8	1148.43	77.18
DG-HB	8.3%	yes	10	2	9	18.05	6	984.014	68.36
DG-HG	2.1%	yes	1	1	6	17.27	5	842.014	79.43
DG-T	2.1%	yes	3	1	3	21.68	5	860.294	70.71
G-W	4.2%	yes	1	0	5	21.52	4	811.744	70.77
HB-T	20.8%	yes	3	0	8	17.75	4	679.714	55.19
HG-L	8.3%	no	0	0	10	18	3	494.292	50.11
R-S	2.1%	yes	0	0	4	15.57	4	541.385	68.86
T-W	0.0%	yes	0	0	1	13.91	6	1342.643	62.25

3.4.3 Temporal Structure: Template Learning?

From the data and figures presented in section 3.4.2, it became clear that most offspring did not copy complete song motifs from adult tutors. Visual inspection of sonograms indicated that they rather learned single syllables or syllable sequences. 15 out of 40 offspring males learned from one tutor. Eleven of them learned all syllables in their repertoires from one tutor and did not have any “new” syllables in their motifs. Five offspring males learned the complete repertoire of the tutor, including the syllable order and (parts of) the temporal structure of the motif, but only 3 of them produced (near) perfect copies of tutor motifs. 25 males learned from more than one tutor and 17 of them also had “new” syllables in their repertoires (table 3.4.4).

Offspring birds that learned from more than one tutor seemed to have one main tutor from whom they not only learned syllables, but also syllable order and to a lesser extent motif structure (temporal pattern and motif duration – fig. 3.4.6). Some offspring however (7 out of 40) seemed to have created a completely new motif.

I then attempted to quantify these observational data by calculating motif similarity scores using SAP (Sound Analysis Pro). For this purpose, 10 song motifs were selected for all offspring and tutors from aviary 2, which was chosen as representative for all aviaries. First I calculated individual similarity scores for all birds (tutors and offspring) and then the between-tutor-offspring similarity scores were calculated (table 3.4.5). Similarity scores were only calculated for combinations of offspring birds with tutors from whom they had

learned at least one syllable (syllable categories 1-4). The results of this analysis are presented in table 3.4.6.

Table 3.4.4: Number of tutors from whom each male offspring per aviary learned (copy, imitation, variation, element) at least one syllable, and average number of tutors that the offspring learned from per aviary.

aviary 1 offspring	no. of tutors	aviary 2 offspring	no. of tutors	aviary 3 offspring	no. of tutors	aviary 4 offspring	no of. tutors
HB-T_W	3	DB-P_W	3	DB-G_W	3	DG-HB_W	4
L-O_G	3	G-G_W	3	G-HG_W	1	DG-L_W	1
L-T_G	1	G-P_W	1	HG-P_HG	4	DG-O_W	1
O-O_G	2	G-S_W	2	HG-P_W	2	DG-R_W	1
O-S_G	3	HB-HG_W	2	HG-R_HG	1	DG-S_W	2
P-P_G	4	HG-O_HG	3	HG-T_HG	3	DG-T_W	4
DB-W_W	4	L-R_G	1	O-P_G	3	HB-HB_W	3
G-W_W	3	P-R_G	1	R-S_G	1	HB-P_W	2
HB-W_W	2	R-R_G	1	S-W_W	2	DB-HG_HG	3
O-W_W	1	T	1			HG-S_HG	3
P-W_W	1						
average	*2.45*	*average*	*1.80*	*average*	*2.22*	*average*	*2.40*

Table 3.4.5: SAP (Sound Analysis Pro) similarity scores (%) for motifs per individual. Values here are averages of MxN comparisons of 10 selected motifs per bird and give an indication for motif consistency. Numbers in the column "from" represent the number of tutors from whom the offspring bird learned at least one syllable (syllable category 1-4).

offspring	**similarity**	**syllables**	**duration**	**from**	**tutors**	**similarity**	**syllables**	**duration**
DB-P_W	68.99	6	1027	3	DB-G	61.85	7	1293
G-G_W	38.43	7	1009	4	DG-DG	77.18	10	1830
G-P_W	93.17	5	774	1	DG-HB	68.36	8	1108
G-S_W	47.32	5	782	2	DG-HG	79.43	6	952
HB-HG_W	52.10	8	1219	2	DG-T	70.71	5	857
HG-O_HG	68.23	6	886	3	GW	70.77	12	1974
L-R_G	74.34	10	1485	1	HB-T	55.19	7	881
P-R_G	76.86	9	1209	1	HG-L	50.11	6	1058
R-R_G	67.56	4	882	1	R-S	68.86	4	779
T	89.07	6	1038	1	T-W	62.25	6	1297

Since the similarity scores for comparisons between offspring and tutor motifs are sensitive to within-bird similarity scores (i.e. consistency), it is difficult to draw conclusions from table 3.4.6 only, which is why table 3.4.5 and figure 3.4.6 should be considered too, although the possible effects of differences in within-bird similarity scores on between-bird scores are not known exactly. The data of the SAP-analysis confirm the observation that some offspring birds learn more from their tutors than just syllables: higher motif similarity scores indicate that the motif was learned better. A remarkable result from the SAP-analysis is that offspring birds that learn from only one tutor generally get higher within-individual similarity scores, indicating more consistent and stable song.

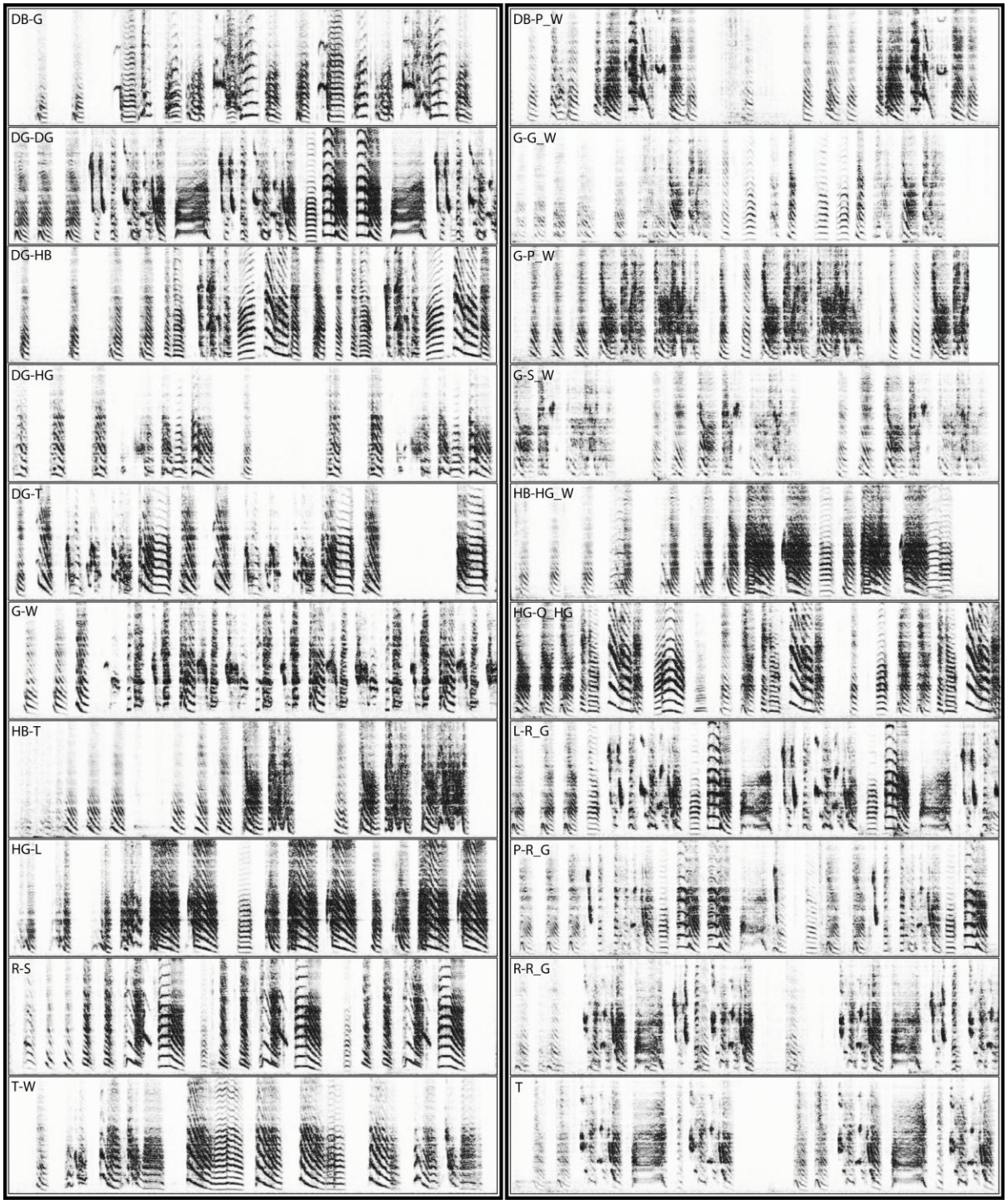

Figure 3.4.6: Sonograms of all birds in aviary 2. Left panel: all adult males. Right panel: all offspring birds. Each sonogram shows a 2500 ms period of song, containing at least one full motif.

Table 3.4.5 shows that within-bird similarity scores are highly variable between birds. I therefore investigated whether these differences in song stability were related to the number of males growing up in the same clutch. Offspring males were therefore divided into two groups: those who were the only male in the clutch and those who had at least one brother (fig. 3.4.7). Although the sample size was low (I only investigated aviary 2 as representative for all aviaries), a normality test and a test for equal distribution of variances were passed, and a two-sample t-test was carried out to test for differences in similarity

scores. However, no significant differences were found (t=-1.246, df=8, p=0.248). I repeated this procedure for motif duration and tested whether there was a difference in motif duration (average from 10 motifs measured per bird) between birds from clutches where they were the only male, in comparison to birds who had at least one brother. A normality test and a test for equal distribution were passed and a two-sample t-test was carried out, which did not reveal any significant difference in motif duration (t=0.530, df=8, p=0.611).

Table 3.4.6: SAP (Sound Analysis Pro) similarity scores (%) for comparisons of motifs between individuals. Values here are averages of similarity scores for 10 selected offspring motifs x 10 selected tutor motifs.

offspring	tutor	similarity
DB-P_W	G-W	47.47
DB-P_W	DG-HG	52.73
DB-P_W	HB-T	55.72
G-G_W	HB-T	55.37
G-G_W	DG-HB	46.17
G-G_W	DG-DG	42.64
G-G_W	DG-T	52.80
G-S_W	HB-T	74.96
G-S_W	G-W	55.09
G-P_W	HB-T	77.88

offspring	tutor	similarity
HB-HG_W	DG-DG	51.71
HB-HG_W	HG-L	92.23
HG-O_HG	DG-DG	54.07
HG-O_HG	DG-HB	74.54
HG-O_HG	R-S	58.35
L-R_G	DG-DG	70.43
P-R_G	DG-DG	67.30
R-R_G	DG-DG	79.15
T	DG-DG	91.46

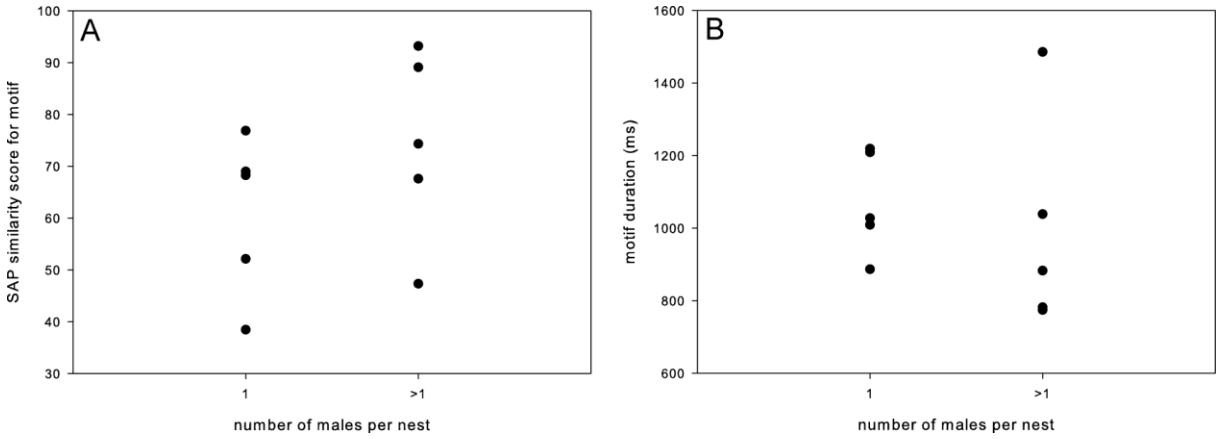

Figure 3.4.7: A) Within-bird SAP (Sound Analysis Pro) similarity scores (%) for offspring males from nests where they were the only males, compared to those for offspring birds from nests with at least one brother. No differences were found. B) Average motif duration (10 motifs) was measured for offspring males from nests where they were the only males, compared to those for offspring birds from nests with at least one brother. No differences were found.

3.5 Experiment 2: Vocal Interactions and Song Development in a Group

3.5.1 Reproduction

Two of the introduced adult pairs switched partners during the first week of the experiment. After this "partner-swapping", relationships were stable and social life in the aviary was harmonious. All three adult pairs raised offspring that survived at least until day 100 post hatching. However, one of the adult males did not have any genetic offspring. One offspring

male (OW) died before day 100 post hatching and the recordings of his vocalisations were not included in the analysis (table 3.5.1).

Table 3.5.1: All offspring produced during the experiment

offspring	sex	nest	hatched	mother	father social	father genetic	offspring ages (days post hatching) at date of analysis 11-Feb	18-Feb	25-Feb	05-Mar	11-Mar	18-Mar
OW	♂	5	26-Oct	T	O	O	108	115	122	130	136	143
TT	♀	5	30-Oct	T	O	O	104	111	118	126	132	139
SW	♂	10	07-Nov	G	S	S	96	103	110	118	124	131
GW	♀	10	07-Nov	G	S	S	96	103	110	118	124	131
WW	♂	10	08-Nov	G	S	S	95	102	109	117	123	130
GG	♂	10	09-Nov	G	S	S	94	101	108	116	122	129
SS	♂	10	11-Nov	G	S	S	92	99	106	114	120	127
LL	♀	7	23-Nov	L	B	S	80	87	94	102	108	115
BL	♂	7	23-Nov	L	B	S	80	87	94	102	108	115
HT	♂	8	07-Dec	T	O	O	66	73	80	88	94	101
OT	♀	8	07-Dec	T	O	O	66	73	80	88	94	101
HO	♂	8	08-Dec	T	O	O	65	72	79	87	93	100
HH	♀	8	09-Dec	T	O	O	64	71	78	86	92	99
BH	♀	8	10-Dec	T	O	O	63	70	77	85	91	98

3.5.2 Song Learning

At day 100 post hatching, all male offspring produced “normal” Zebra Finch song (fig. 3.5.1). All categories of learned syllables (1-4) were found in the total repertoire, but the birds did not produce any new syllables (category 5). Four (out of seven) males learned from more than one tutor, but all of them clearly learned from one main tutor (table 3.5.2). As in experiment 1D, syllable sharing among offspring was common and also the general learning results were comparable.

Table 3.5.2: Song learning per offspring bird and per category. Category 1 = copy, 2 = imitation, 3 = variation, 4 = element. For each category, the number of learned syllables is given, followed by the tutor from whom they were learned (tutor). The row “shared” gives the number of siblings with whom the offspring bird shared at least one of his syllables.

	category 1		category 2		category 3		category 4		shared
BL					6 (B)		3 (B)		0
HO			2 (O)		4 (O)				0
GG	3 (S)		2 (S)		2 (S)	1 (B)			4
SS	5 (S)		1 (S)		2 (S)				3
WW			1 (O)	2 (S)	1 (B)	1 (S)	1 (S)		1
SW	1 (B)	2 (S)			1 (S)		2 (S)		4
HT	1 (B)		2 (O)						1

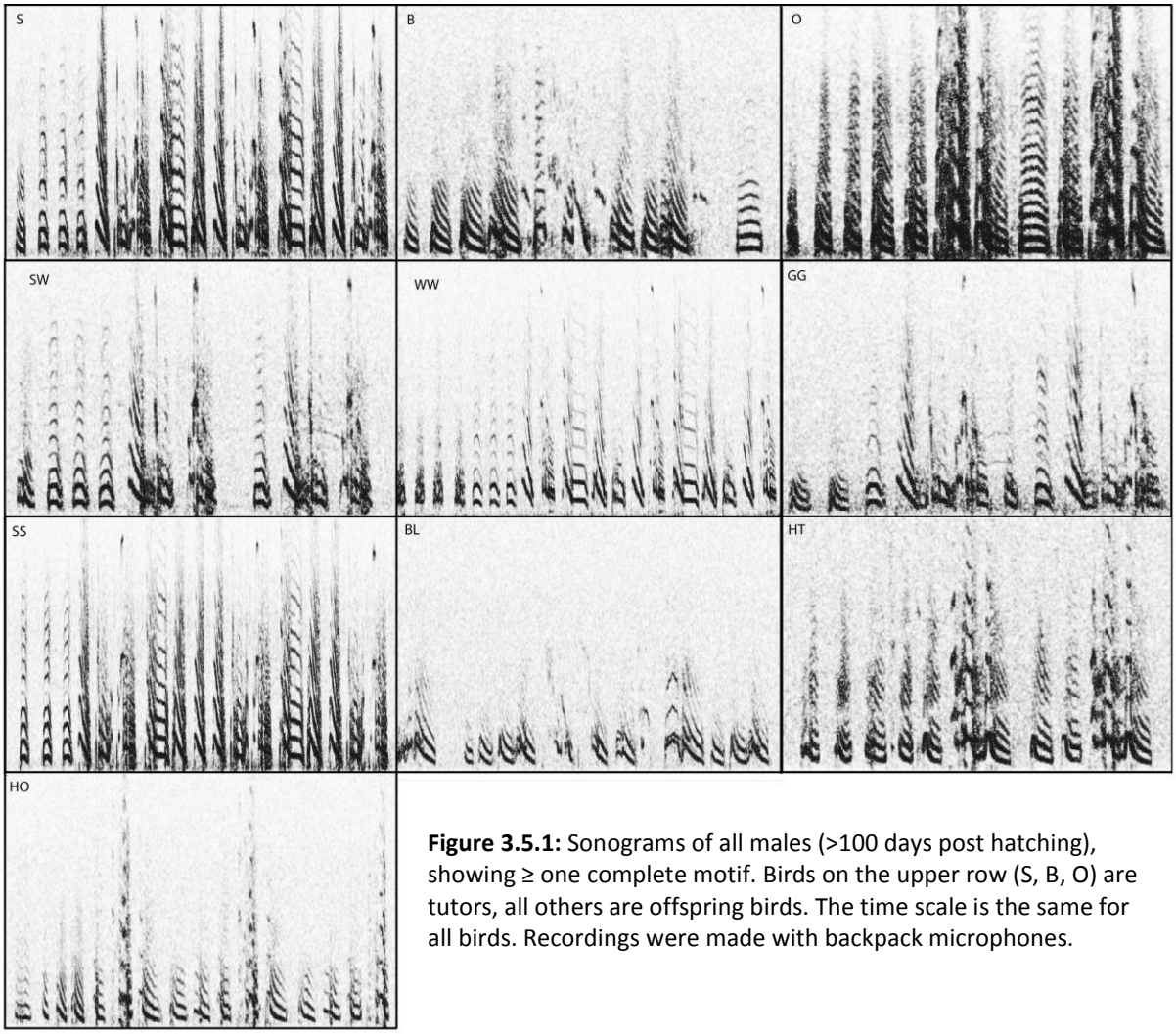

Figure 3.5.1: Sonograms of all males (>100 days post hatching), showing ≥ one complete motif. Birds on the upper row (S, B, O) are tutors, all others are offspring birds. The time scale is the same for all birds. Recordings were made with backpack microphones.

3.5.3 Social Interactions

For some of the birds that were equipped with backpack microphones, no recordings are available for one or two of the six selected days (see table 3.5.3), which was due to technical difficulties. This was corrected for in the total calculations of interaction intensities. From the plots shown in fig. 3.5.2, it becomes clear that some birds are involved in more social interactions than others.

The total numbers of vocalisations (total of all song syllables and calls) produced per day are variable (table 3.5.3) and differ between birds (One Way ANOVA $F=2.253$, $p=0.029$). However, a Tukey Post Hoc test (pairwise comparisons) revealed that this result was caused only by the differences between tutor B and offspring WW and SS: all other pairwise comparisons did not yield any significant differences.

Table 3.5.3: total number of vocalisations (tested clusters + remaining clusters) per bird per day. Vocalisations are defined as song syllables AND calls.

	11-Feb	18-Feb	25-Feb	05-Mar	11-Mar	18-Mar	average
S	18542	17458	1970	3796	11388	no data	10631
B	7609	6905	11248	5109	5640	1717	6371
O	no data	11788	16184	8224	no data	4766	10241
BL	9019	5438	no data	24700	18543	11814	13903
HO	20185	8294	20201	33965	19791	564	17167
GG	15140	no data	24806	19998	15234	12103	17456
SS	20118	17915	16422	22382	26391	15939	19861
WW	26640	20068	20943	no data	no data	17727	21345
SW	23914	10009	18321	7326	19761	14751	15680
HT	1559	21279	19562	21404	6259	16547	14435

From fig. 3.5.2G it becomes clear that in total (sum of all analysed days) most social interactions in our study group of Zebra Finches occur between siblings, with those between the brothers from nest 10 (SS, SW, WW and GG) being the strongest. All offspring birds interacted more with other youngsters than with any of the adult tutors. Interactions between adult tutors did occur, but were much weaker than those between offspring birds.

The overall interactions between offspring and tutors were not very clear and/or consistent in most cases. At first glance it looked as if the young birds interacted more with one particular tutor than with the others, in most cases with their father and/or song tutor. Statistical analysis (Kruskal-Wallis One Way Analysis of Variance on Ranks – all pairwise multiple comparisons: Dunn's method) revealed that 3 out of 7 offspring birds interacted significantly more with one specific tutor than with the other two (table 3.5.4). One of these birds, BL, interacted most with his social father B, who was also his main tutor. Offspring HO also interacted most with tutor B, whereas offspring SW interacted most with tutor O. This is remarkable, since these offspring-tutor dyads were not related in any way and the offspring birds did not learn from the said tutor either.

Table 3.5.4: overall average number of significant interactions between selected offspring and tutor clusters per offspring bird, irrespective of strength of interaction. Bold numbers indicate that the offspring bird interacted significantly more with this tutor than with the other two.

	S	B	O
BL	3.3	**4.2**	2.3
HO	2.8	**3.5**	2.5
GG	4.8	4.6	5.0
SS	3.6	3.7	3.0
WW	5.7	3.5	6.0
SW	4.0	4.3	**5.5**
HT	3.4	3.5	3.0

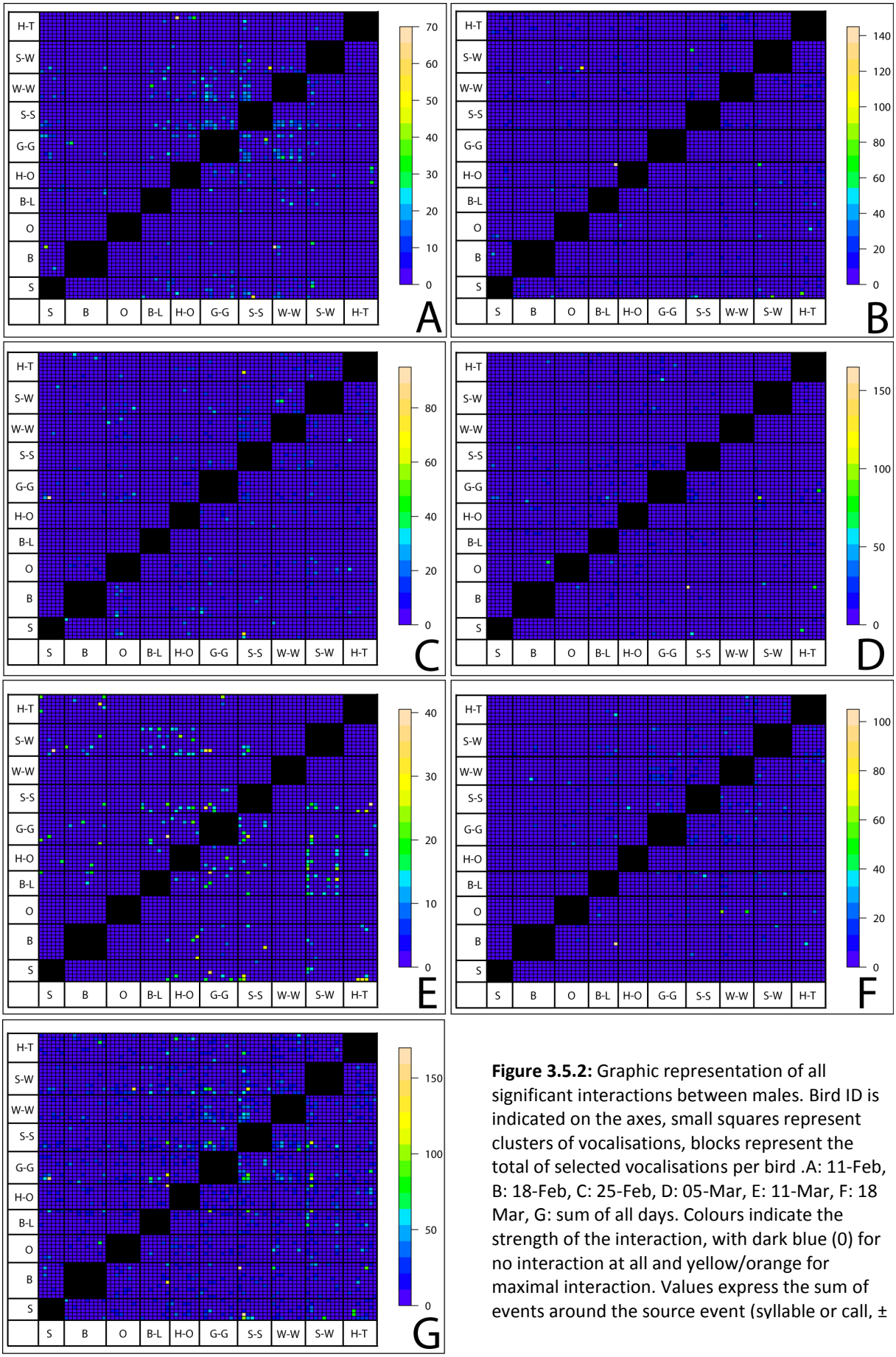

Figure 3.5.2: Graphic representation of all significant interactions between males. Bird ID is indicated on the axes, small squares represent clusters of vocalisations, blocks represent the total of selected vocalisations per bird .A: 11-Feb, B: 18-Feb, C: 25-Feb, D: 05-Mar, E: 11-Mar, F: 18 Mar, G: sum of all days. Colours indicate the strength of the interaction, with dark blue (0) for no interaction at all and yellow/orange for maximal interaction. Values express the sum of events around the source event (syllable or call, ±

Chapter 4

Discussion

4.1 General Considerations

Zebra Finches are highly social and live in groups. Since humans live in groups too, we tend to think of it as natural and advantageous, but in fact social species are relatively rare. Living in groups is not as easy as it seems: it requires clear social structures, communication and coping with adversity. The benefits of social life only become clear under specific circumstances. Alcock (1998) describes it as follows: *"In animal societies, individuals tolerate the close presence of conspecifics despite the increased competition for limited resources and the heightened risk of disease that it entails. Under some ecological circumstances, the advantages of sociality (usually improved defence against predators) are great enough to outweigh the many and diverse costs of social living."*

The social environment in which an individual lives has a great impact on various aspects of its life and fitness. A clear example to underline this statement is provided by the results of experiment 1A: it shows that differences in population density only, can already cause clear differences in various physiological and behavioural parameters between groups of captive Zebra Finches, even though essential resources (food, water) are provided *ad libitum*.

In this thesis I mainly focus on the social factors that influence the process of song learning and tutor choice in groups of songbirds, and use the Zebra Finch as a model species. Studying song learning in the field is difficult, since Zebra Finches live in large flocks and are exposed to many tutors and involved in diverse and complex social interactions (Zann 1996). In order to at least approach a semi-natural setting, experiments were carried out with groups of domesticated Zebra Finches in aviaries. I used different aviary sizes, which enabled me to study the effects of population density, an important factor in natural populations, on physiology, social behaviour and song learning. Although the experiments took place under controlled laboratory conditions, some careful extrapolations could be made which allow statements about Zebra Finches in general. In this chapter I discuss the findings presented in Chapter 3 with special focus on song learning and tutor choice. Furthermore, I try to give an indication for the direction of future research in multi-tutor environments.

Over the last 50 years, several hypotheses to explain tutor choice in Zebra Finches have been tested (Derégnaucourt 2011; Zann 1997). The predominant one is that juveniles learn from their fathers, although alternative hypotheses like the importance of tutor pairing status, colour morph, song rate and quality, level of aggressiveness, etc. have been put forward and tested as well. Experiments focusing on single hypotheses have been carried out mostly with (isolated) birds in cages and groups of various sizes and composition in aviaries. However, so far the question if and why juveniles learn from certain tutors has not been answered satisfactory and with this thesis I want to contribute to solving it.

For this purpose I studied social groups of Zebra Finches and tested whether juveniles really prefer certain tutors, or if they randomly learn single song elements that they hear in their environment. In all of my experimental aviaries (4 from experiment 1 and 1 from experiment 2), I found that juvenile Zebra Finches show significantly clear and consistent tutor preferences, which is the first confirmation of tutor choice under semi-natural conditions. Then I investigated why certain tutors are chosen and what makes the preferred tutors stand out from the crowd: behaviour, looks, song characteristics, social interactions, or maybe something else altogether?

4.2 Population Density (experiment 1A)

4.2.1 Social Behaviour

Absolute numbers of social interactions were higher in high density than in low density aviaries, which is probably a real density effect. When looking closer at the type of interactions that take place under both density conditions, some other interesting results emerge.

The levels of aggression observed during the experiment were generally low, which may be due to the fact that observations started one week after the birds were introduced to the experimental aviaries and a social structure was already established by then. The higher numbers of aggressive interactions in high density aviaries may be explained mostly by increased intensity of nest defence (Caryl 1975; Evans 1970; Zann 1996). Although the nest boxes were positioned at the same height in all experimental aviaries, in high density aviaries the distance between boxes was only half of the distance between boxes in low density aviaries (Fig. 2.1). Although this result is remarkable, the trend towards higher numbers of affiliate interactions in low density conditions may be even more interesting.

The predominant behaviour within this category of affiliate interactions is allopreening, which was observed between male-female, but also between female-female and to a lesser extent male-male dyads. Allopreening, like grooming in primates, probably has an important social, as well as hygienic function. It is believed to alleviate stress and strengthen social bonds between individuals (Aureli & Yates 2010; Henzi & Barrett 1999; Watts 2000; Wittig *et al.* 2008). In studies with different species of primates it was found that individuals that are exposed to stress increase the intensity of allogrooming in order to relieve tension and prevent aggression (Schino *et al.* 1988; Terry 1970). I expected that allopreening in Zebra Finches has a similar function, which is why I expected higher numbers of affiliate interaction in high-density aviaries. The actual result was therefore rather surprising.

4.2.2 Song Complexity

The most striking differences between the high and low density experimental aviaries were found in song complexity (total number of syllables and motif duration) of offspring, confirming the results of a previous study carried out at the Free University of Amsterdam (Gahr, pers. comm.). Birds in low density aviaries developed longer song motifs, which consisted of more syllables per motif.

In an experiment with two 3x3x2m aviaries (low density), Mann and Slater (1995) did not find an indication for differences in song complexity between offspring and tutors, but Williams (1990) found that offspring in a 4x2.5x2m aviary (low density) produced more complex songs than the adult tutors. However, neither Mann and Slater (1995), nor Williams (1990) tested for population density effects. Williams' explanation for the difference in song complexity between offspring and tutors was that the adult tutors used in her experiment probably produced impoverished songs, since they were raised in single cages with physical access to only one song tutor. Song motifs of such males are consequently shorter and less varied than those of wild or aviary-raised males (Williams 1990). The tutors used in the current study, however, were all raised in the presence of multiple song tutors.

The differences found in my study could at least partially be explained by the higher number of repeated syllables per motif in the low-density offspring, which was not the case in Williams' study (Williams 1990). In consequence, the number of learned syllables did not

differ between pupils of high and low density aviaries. Thus, if we consider that stress has negative effects on song development and learning (Woodgate *et al.* 2011, but see Gil *et al.* 2006), this finding is a first indication that the used population densities do not cause severe stress to the birds.

4.2.3 Corticosterone

Unlike in colonies of cliff swallows, where adult baseline corticosterone levels increase with group size (Brown *et al.* 2006), no significant relation was found between corticosterone levels and population density in Zebra Finches. Mean levels in all aviaries ranged between 1 – 3.3 ng/ml, but great individual variation was observed. This suggests that population density in the experimental aviaries did not cause extreme stress to the birds. Furthermore, it indicates that corticosterone does not explain the variation in body mass (adults, offspring) and size (offspring), as well as offspring survival and song complexity and –duration.

The relatively high corticosterone levels in nestlings (on 15 dph) might indicate that they are exposed to higher stress levels than juveniles that have already fledged, although it could also be an indication for increased energetic demand or other developmental issues. A similar pattern was found by Wada *et al.* (2008), who measured corticosterone levels at 16 days post hatching and explain the elevated levels by the nestlings' proximity to fledging.

4.2.4 Brood Size Effects

On day 15 post hatching, a positive correlation was found between brood size (i.e. density in the nest) and offspring baseline corticosterone levels, which may be an indication for higher stress levels in larger broods. This is in line with findings in blue tits (Lobato *et al.* 2008), pied flycatchers (Ilmonen *et al.* 2003), and tree swallows (Parsons & Vleck 2009), but see Gil *et al.* (2008) for spotted starlings. The differences in corticosterone levels between offspring from different brood sizes levelled out during development, and were no longer measurable on day 60 and 100 post hatching. Gil *et al.* (2006) found that nestlings in large broods were lighter (body mass) and smaller (tarsus length) on day 10 post hatching, but these differences disappeared when the offspring reached adulthood. No corticosterone levels were measured in their study, but it is possible that the differences found on day 10 post hatching were related to corticosterone, with higher plasma levels in larger broods inhibiting growth.

Compensatory growth is a well-known phenomenon in Zebra Finches, which could be a result of, but not a cause for increased levels of corticosterone (Honarmand *et al.* 2010). It is possible that on day 15 post hatching, initial differences in body mass and size, as found on day 10 post hatching (Gil *et al.* 2006) have already levelled out due to compensatory growth in offspring from larger broods.

4.2.5 Fitness Effects?

Body size seems to be an important criterion in mate choice, with larger birds being preferred over smaller ones (Ikebuchi & Okanoya 2006; Riebel 2009; Tomaszycki & Adkins-Regan 2005). The larger increase in body mass found in low density aviaries could therefore indicate higher fitness. Another indication therefore is that birds in low density aviaries produced more offspring surviving until at least day 100 post hatching, although it cannot be excluded that both factors (body weight and reproductive success) are correlated. The

fact that offspring in low density aviaries was significantly larger (tarsus length) and heavier (body mass) than in high density aviaries is another indication for a fitness difference between birds living in high and low population density conditions. The trend towards a female biased sex ratio in low-density aviaries could also be interpreted as an increased potential for more offspring in the next generation. The increase in body mass of adult birds that occurred in all aviaries indicates that the birds were all in good condition.

The difference in song complexity may be another indication for a fitness advantage for offspring growing up under low density conditions, since song complexity is also thought to be an important criterion in mate choice (Ikebuchi & Okanoya 2006; Riebel 2009; Tomaszycki & Adkins-Regan 2005), with females preferring males that sing more complex song (Catchpole & Slater 1995; Spencer *et al.* 2004). I expected that males, who are preferred by females and produce many offspring, would also be preferred by juveniles as song tutors. Nevertheless, fitness in terms of number of surviving offspring did not affect tutor choice (section 3.4).

4.2.6 Conclusions from Experiment 1 A

If conditions are harsher and resources get scarce, birds congregate around the resources that are still available and population density locally increases. At high population density, individuals are increasingly confronted with the adverse effects of group life, like spreading of diseases and parasites and of course competition (Krebs & Davies 1993). However, even in the high-density aviaries the birds did not experience many adverse effects, as stress levels were low in all aviaries: no differences were found in baseline plasma corticosterone levels and the general behaviour displayed by the birds was normal. The results of this experiment indicate that birds (both adults and offspring) in high density aviaries are all in good condition and are not behaviourally or developmentally impaired in comparison to birds in other studies (Boag 1987; Cuthill *et al.* 1997; Dall & Witter 1998; Gil *et al.* 2006). However, birds in low density aviaries did better with respect to physical condition (adults grew heavier) and produced more (surviving) offspring, which grew bigger and heavier and produced more song syllables and longer motifs.

The current findings, therefore, underline the importance of designing appropriate housing conditions for Zebra Finches in order to optimise wellbeing and perhaps even fitness, which is beneficial to breeders, pet owners and scientists alike. Furthermore, these results prove that the legal guidelines for keeping Zebra Finches (EU 2007), as implemented in Germany, are sensible.

4.3 Social Structures and Dominance Hierarchies (experiment 1B)

4.3.1 Correlations between Dominance and Physiological & Behavioural Traits

Although clear patterns were observed, no strictly linear dominance hierarchies were found in the experimental aviaries. This could be due to the high number of inconsistencies in the hierarchies, indicating triangular dominance relationships (De Vries 1993) or to the relative high number of unknown relationships between birds, which could have been improved by more and/or longer observation periods per bird. Since dominance hierarchies are usually formed within days (Chase 1982) and most aggressive interactions occur in this period, the level of aggression I observed during the observation periods was relatively low. Unfortunately, I was not able to collect data in the first ten days of the experiment.

In the present study, behavioural rank and perching position were positively correlated. More dominant animals generally occupied higher perching positions, even though perches were large enough (75 cm) for all 20 flock members to sit next to each other. This was expected based on observations of different species of birds preferring positions on the highest perches or branches, both in captivity and in the wild. However, to my knowledge, no scientific evidence is available so far on the relation between social dominance and perching position in songbirds. Most studies on correlations between dominance and perching have been carried out with lizards (Radder *et al.* 2006; Zucker 1986). Evans & Sordahl (2009) proved that Turkey vultures also prefer higher perching positions and showed that the highest perches are significantly more occupied by older birds, indicating an age-dominance-effect. Cordiner & Savory (2001) studied the relationship between dominance and perching in Brown hens, which usually spend most of the time on the ground, gathering food. When perches and nest boxes are available, it was found that lower ranking birds make more use of perches and to a lesser extent nest boxes during daytime, whereas these are mostly occupied by higher ranking birds at night (Cordiner & Savory 2001). Although this is a very interesting result in itself, possible relationships between dominance and perching heights are not investigated.

The weak positive correlation between behavioural rank and body mass was not unexpected, since there is evidence that bigger animals are more likely to become dominant in various bird species (Lindstrom *et al.* 2005; Robinson-Wolrath & Owens 2003; Senar *et al.* 2000; Shoemaker 1939). Furthermore, female Zebra Finches prefer bigger males in mate choice (Ikebuchi & Okanoya 2006; Riebel 2009), which is another indication that larger body size is advantageous in Zebra Finches.

More surprising was the trend towards lower song complexity (fewer syllables per motif; shorter motif duration) in bigger males, even though behavioural rank was not significantly correlated with song complexity as it is in European Starlings (Spencer *et al.* 2004). There is evidence that female Zebra Finches prefer males that produce more complex song when presented with different song motifs (Riebel 2009). This would imply a disadvantage for males that produce less complex song and potentially limit their reproductive success. However, physiological traits (body size, plumage) are probably stronger criteria for mate choice than song complexity (Ikebuchi & Okanoya 2006). It is possible that smaller birds compensate for their optic disadvantage by means of acoustic signals and thus produce more complex song. Although my study does not provide sufficient evidence to support this hypothesis, it would be interesting to test this in the future.

Within the framework of finding out why juvenile Zebra Finches preferentially learn from certain tutors, I tested whether offspring birds learned more from higher ranking males (section 3.4), who are generally more aggressive than others, or from heavier males. However, I did not find any clear relationships.

4.3.2 Importance of Dominance

From experiment 1B it becomes clear that even though dominance has been studied for many years, relatively little is known about the mechanisms and functions of dominance hierarchy formation in either captive or wild flocks of Zebra Finches. The fact that Zann (1996) did not find linear dominance orders in a specific population of wild Zebra Finches also does not mean that social dominance structures do not occur in Zebra Finches. It is well possible that dominance hierarchies only become more important when conditions are

harsh and resources limited (Carrascal *et al.* 1998; Heinrich 1994) as is sometimes the case in wild, but not in captive populations.

Clear dominance patterns could help prevent, or at least reduce aggressive interactions. Under harsh conditions, individuals would compete more strongly over dominance since a high rank, especially in males, is often associated with priority access to resources (Banks *et al.* 1979) and increased reproductive success (Dewsbury 1982; Ellis 1995), and sometimes vice versa (Lamprecht 1986a, b). For Zebra Finches, such relationships have not been proven so far, but it remains interesting to investigate social behaviour in relation to dominance patterns.

In captive populations, all group members are theoretically able to reproduce successfully, since resources are plenty (Beauchamp 2006; Ekman & Lilliendahl 1993). This could explain the results of my study, where no correlation was found between reproductive success (number of offspring per individual) and behavioural rank, body size or song complexity. It would therefore be interesting to study social dominance in populations that only have limited resources at their disposal.

4.3.3 Conclusions from Experiment 1B

The theory that dominance hierarchies are not as relevant and therefore less strict in captive populations than in the wild may also explain why no clear correlations were found between behavioural rank and baseline corticosterone levels (Creel 2001; Poisbleau *et al.* 2005). It could be expected that lower social rank implies more stress and subsequently higher (baseline) corticosterone levels. In situations where resources are limited, lower ranking individuals usually have limited access to various resources or are only able to obtain resources of inferior quality (Banks *et al.* 1979). However, in my experiment resources are not limited and the disadvantages for lower ranking birds are probably not severe enough to cause significant increases in baseline corticosterone levels.

The dominance hierarchies found under the current conditions probably only serve as a means to facilitate group life and reduce numbers of agonistic interactions. In order to make clearer statements about the existence and importance of dominance hierarchies in Zebra Finch populations, more research will be necessary.

4.4 Behavioural and Reproductive Patterns (experiment 1C)

4.4.1 Pair Bonding

Zebra Finches are monogamous birds that usually form strong long term pair bonds both in the wild and in captivity (Butterfield 1970; Silcox & Evans 1982; Zann 1996). There is evidence that the process of pair formation starts within 30 minutes of the introduction of unfamiliar Zebra Finches (Silcox & Evans 1982) and it is assumed that it only takes several days to fully establish a pair bond (Ikebuchi & Okanoya 2006; Silcox & Evans 1982; Tomaszycki & Adkins-Regan 2005; Zann 1996). As described in Chapter 2, all males had spent at least 2 days with a designated female in soundboxes before my experiment started. However, only 2 of these pairs stayed together throughout the experiment, which may be due to the fact that pair bonds had formed before the soundbox-experience, or handling stress which prevented pair bonding in soundboxes. During the experiments, stable pair bonds did develop between many individuals. The establishment of a homosexual pair in one of the experimental aviaries was remarkable but not unique (Bailey & Zuk 2009;

Ikebuchi & Okanoya 2006; MacFarlane *et al.* 2007). According to Zann (1996), Zebra Finches select a pair bond rather than remaining single even when no desirable partners are available. This theory seems appealing because we humans can comprehend intuitively that nobody wants to be lonely. Furthermore, Adkins-Regan & Tomaszycki (2007) found strong indications that continuous pairing can speed up initiation of reproduction. The presence of unpaired birds and single-parent nests in all aviaries is therefore more difficult to explain.

4.4.2 Extra-Pair Offspring

Despite the fact that Zebra Finches, like many group living species, are socially monogamous, extra pair copulations (EPC) resulting in extra pair offspring (EPO) are not uncommon. Males are generally assumed to benefit from having extra-pair offspring, since it offers them the opportunity to pass on their genes at low costs. Females generally invest more energy in producing and raising offspring than males, which is why spreading chances by copulating with more than one partner could also be a good strategy. The only way to be confident about parentage is DNA-analysis of all individual group members.

The total proportion of EPO (16.5%) found in my experimental populations was much higher than in wild populations, where the rate of EPO does not exceed 3.3% (Birkhead *et al.* 1990; Griffith *et al.* 2010). However, this relatively high number was not completely surprising considering the fact that in previous studies on captive Zebra Finches, numbers of extra-pair offspring were found to be higher than in the wild as well. The proportion of EPC could even have been higher, since it cannot be excluded that more birds engage in EPC than expected based on the numbers of EPO: it is well possible that most cases of EPC go unnoticed (Fossoy *et al.* 2006), although it is highly unlikely that all birds in a population engage in EPC.

Having EPO can be advantageous: the results of a study on Tree Swallows, (Dunn *et al.* 2009) suggest that the presence of at least one EPO per nest increases the immune response of the entire clutch and thus increases fitness, which could be an explanation for the occurrence of EPC and EPO. However, it does not explain the differences in rates of EPC and EPO found between wild and captive populations of Zebra Finches.

A common explanation for differences in rates of EPC and EPO within species is the intensity of mate guarding, which prevents cheating (Arcese 1989; Birkhead *et al.* 1989; Dias *et al.* 2009). Based on this hypothesis, it would be expected that the confined aviary environment with limited hiding space (no trees or shrubs were available) and the availability of *ad libitum* food and water facilitates mate guarding, resulting in lower numbers of EPC and EPO. Since the opposite is true for my study populations, it is unlikely that mate guarding explains the differences in rates of EPO between wild and captive populations of Zebra Finches.

Furthermore, it is not likely that the relatively high rates of EPO found in captive populations of Zebra Finches are an artefact of the process of domestication (Forstmeier *et al.* 2007b): although captive populations of Zebra Finches have lost some of the genetic variability present in the wild, this is probably caused by random loss of rare alleles.

I tested whether juvenile Zebra Finches preferentially learn from adult tutors who produced EPO, since having EPO could be interpreted as an indication of male quality, but did not find any clear relationships.

4.4.3 Adaptive Strategies?

An alternative explanation for the differences in numbers of EPO between wild and captive populations would again be the difference in environmental conditions. Numbers of extra-pair offspring are generally expected to increase with resource abundance (Griffith *et al.* 2002), whereas under harsh conditions, numbers are lower and the need for biparental care and strong (monogamous) pair bonds increases. This could even be related to the existence of alternative reproductive strategies: it is possible that the different categories of reproductive and behaviour patterns found in all aviaries (categories: 1) monogamous pair *with* offspring, *without* EPO; 2) monogamous pair *with* offspring, *with* EPO; monogamous pair *without* offspring; 4) single *with* EPO; 5) single *without* offspring) represent different reproductive strategies, that are adaptive to specific environmental conditions.

The best-known example of a bird species which follows different reproductive strategies according to different environmental conditions is the Dunnock (Davies & Lundberg 1984), but evidence for adaptive strategies is also found in e.g. Tree Swallows (Dunn & Hannon 1992) and Bricknell's Thrush (Goetz *et al.* 2003), and supported by theoretical models (Fromhage *et al.* 2005). Normally numbers of EPO are expected to increase and the time spent on the provision of parental care is expected to decrease when resources are abundant, but Vaclav *et al.* (2003) found that House Sparrows provided with additional food produced less EPO and especially the females provided more parental care.

In some species, the benefits of different reproductive strategies vary between the sexes (Dias *et al.* 2009; Forstmeier 2007). Arcese (1989, Song Sparrow) and Moskwik & O'Connell (2006, Bobolink) found that polygynous males raised more young than monogamous ones, whereas monogamous females raised more young than those living in polygynous groups. In our study populations of Zebra Finches, no sex differences in reproductive success per strategy were found.

4.4.4 Conclusions from Experiment 1C

From the results of my experiment it may be concluded that maintaining a monogamous pair bond AND engaging in extra-pair copulations optimises reproductive success in an aviary environment with *ad libitum* food and water and limited nest space. In wild populations however, it seems advantageous to be strictly monogamous (Birkhead *et al.* 1990; Griffith *et al.* 2010). A recent study proved that individual differences in extra-pair mating behaviour in Zebra Finches have a hereditary component which is shared between the sexes (Forstmeier *et al.* 2011). The main aim of experiment 1C was to discuss an idea and collect preliminary data. To find out whether different reproductive and behaviour patterns observed in Zebra Finches reflect different reproductive strategies, more research is necessary. For example, it is important to know if the reproductive and behaviour patterns found in this study are consistent. Therefore, birds have to be allowed to produce multiple broods, and also the following generations need to be followed. Furthermore, it is interesting to study if the same patterns emerge in other captive flocks of Zebra Finches.

In order to test if the patterns I found are adaptive, it is also crucial to compare populations in different environmental conditions, for example by food restriction, limited nesting opportunities, or unequal numbers of males and females. Furthermore brood size manipulation and/or cross-fostering can be used to test possible relationships between reproductive strategy and reproductive success. In order to make clearer statements about reproductive strategies and -success, it would also be interesting to not only test the genetics of chicks, but also of the eggs that did not hatch.

4.5 Song Learning and Tutor Choice (experiment 1D)

4.5.1 Song Learning: What and How?

The aim of experiment 1D was to investigate what juvenile Zebra Finches in a multi-tutor environment learn from whom, and here I also focused on the question how they learn. It is generally assumed that young Zebra Finches aim to copy the complete motifs of one tutor and in the book "Animal Innovation", Slater & Lachlan state: "*Learning can be remarkably accurate, but even in such cases new variants arise not infrequently and, in birds with large repertoires of songs, it is usual for the precise combination of songs that a bird has in its repertoire to be unique."* (Slater & Lachlan 2003) Their explanation for this process is that although juveniles try to copy adult song, which could eventually lead to conformity, innovation in bird song occurs through copying errors and is not actively selected for (Slater & Lachlan 2003).

Irrespective of what is learned, be it complete motifs or only syllables, an important finding of my experiment is that juvenile Zebra Finches that are exposed to multiple tutors show clear tutor preferences. In this experiment, I considered behavioural and physiological traits of the potential tutors, and investigated some acoustic features of tutor song that were thought likely to explain why juvenile Zebra Finches learn more from certain tutors than others.

4.5.2 Does the Number of Potential Tutors Affect Song Learning?

A surprising result from experiment 1D is that 62.5% of all juveniles learned from more than one tutor although most of them had one main tutor, and only 7.5% of all juveniles produced a near perfect copy of a tutor motif. Growing up in a multi-tutor environment has several consequences which could influence song learning. Juveniles have much more vocal input than in single-tutor settings and they do not only hear one tutor, but probably combinations of songs and calls of several adults at the same time. Combinations are never the same in acoustic and temporal structure. Furthermore, focusing on one individual becomes more difficult when group size increases and vocalisations are jammed.

The juveniles that were exposed to only 3 tutors in the experiment with the backpack-microphones (experiment 2) seemed to learn better (more precise and more from the same tutor) than those in the first experiment. This may be due to the difference in tutor abundance, or the acoustic jamming, but it is also possible that the process of learning from more than one tutor leads to reduced learning success. For the first two possibilities I need to see if simultaneous singing occurs, which causes the songs overlap. This would require further analysis of the current data (experiment 2), as well as obtaining continuous recordings from larger groups of animals.

Concerning the learning from multiple tutors, juveniles who learned from two tutors learned better in the second than in the first experiment. A preliminary conclusion would therefore be that that learning from several tutors per se does not reduce the learning success, but the environmental conditions play a crucial role.

4.5.3 Tutor Choice: A Behavioural Ecologist's Point of View

Most male offspring in the experimental aviaries learned from more than one tutor, but also displayed clear preferences for certain tutors. An early indication for such a process was found by Williams (1990), who observed song learning and tutor choice in an aviary with 10 breeding pairs and 2 non-breeding males and found that juveniles imitated all adult tutors,

but not to the same extent: there were 2 clear favourites. In her experiment, most juveniles also imitated syllables from at least two tutors.

In laboratory experiments, Eales (1987a) found that tutor song quality and the possibility to interact visually and vocally with the tutor are of critical importance for song learning in Zebra Finches. Soma *et al.* (2009) stated that tutor choice in Bengalese Finches is influenced by the song complexity of tutors and that it could be adaptive for offspring males to learn from more than one tutor when the repertoire of the tutor(s) is limited. However, this is not a plausible explanation for my results, since all 40 tutors present in the experimental aviaries were raised in a social environment and performed normal Zebra Finch song. Another argument against this hypothesis is that Williams *et al.* (1993) found that in an aviary with song tutors that produced both tutored and untutored song, offspring males learned just as much or more from the untutored song tutors.

The observed preference for certain song tutors in my experiments leads me to reconsider the question how juvenile Zebra Finches in a multi-tutor environment choose a song tutor. Most of the offspring males in our experimental aviaries did not show a preference for either the genetic or the social father, and there did not seem to be a preference for those tutors with highest reproductive success (number of offspring), or the most dominant males in either of the aviaries (table 3.4.3).

Burley (Burley *et al.* 1982; Burley 1985) showed that leg band colour plays a role in mate choice, with female Zebra Finches preferring males with red and seemingly avoiding birds with green leg bands, and some colours being neutral (Burley, pers. comm.). However, the results of my study do not lead to the expectation that tutor leg band colour is an important criterion for tutor choice. All tutors were wearing two coloured leg bands and a metal ring, and juveniles were equipped with three coloured leg bands and a metal ring (bird ID codes represent colour combinations: description in appendix).

My data do not support the hypothesis that juvenile Zebra Finches prefer paired over unpaired song tutors (Mann & Slater 1994, 1995): juveniles learned from paired and unpaired tutors alike. Since all potential song tutors were of the same colour morph, the hypothesis that juveniles prefer song tutors of the same morph as their fathers (Mann & Slater 1994, 1995) can also not explain the observed tutor preferences. As shown in fig. 3.4.5, syllable sharing among peers is quite common, but it is very unlikely that juveniles choose their brothers as song tutors (as is the case in Starlings: Bertin *et al.* 2007), since the age differences were too small and the brothers did not yet produce crystallised song when the younger ones start learning. However, it is well possible that they influence each other during the process of song learning.

The large variations found in within-individual similarity scores for motifs, indicating differences in song consistency, were very interesting as well. I investigated whether these differences were related to the number of males growing up in the same clutch, but found no indications therefore. Since Tchernichovski and Nottebohm (1998) found that males who have brothers in the same clutch produce song with shorter relative motif duration and learn less well than those without brothers, I also investigated possible relations between the presence of male siblings and motif durations. However, I could not confirm this with my data: no differences were found between males from clutches where they were the only males, compared to males from clutches with at least one brother. Although I only measured absolute and not relative (to tutor) motif duration, I do not expect the results to be any different from those presented here.

I did not investigate whether offspring from clutches without male siblings learn better (i.e. have higher between-individual SAP similarity scores with their tutors) than those from clutches with at least one brother, nor whether hatching order has an effect, but I do not expect any differences here either. The fact that such effects were found by Tchernichovski and Nottebohm could be an artefact of holding the birds in cages with only one male tutor, which do not occur under (semi-) natural conditions. However, I do not argue that the social environment plays an important role, and that, as stated by Tchernichovski and Nottebohm, model abundance could be an explanation for differences in song learning.

Analysis of the data of aviary 2 (which was chosen as representative for all aviaries) showed that neither the motif duration, nor the total number of syllables per motif, nor the song consistency (in terms of motif similarity score) of the preferred tutors differed from those of the other (non-tutor) males. Alternative hypotheses as to why certain song tutors are preferred over others are that juvenile Zebra Finches possibly learn from the tutors that sing most (Zann 1996, but see Tchernichovski *et al.* 1999) or loudest, as preferred by females (Ritschard *et al.* 2010), or motif repetition rate. However, since song learning, at least in single tutor environments, requires hearing only a few hundred tutor songs (Leitão, pers. comm.); the latter hypothesis is rather unlikely to explain tutor preference.

4.5.4 Tutor Choice: A Neurobiologist's Point of View

The results of my study indicate that most offspring learn single syllables rather than syllable sequences or complete motifs, which is rather surprising. Juvenile Zebra Finches are generally thought to learn their songs by imitation of adult motifs and are expected to produce more or less perfect copies of complete adult motif (Derégnaucourt 2011; Williams 2004). Those birds that do not copy tutor motifs are usually classified as "bad" or "poor" learners (Derégnaucourt 2011; Houx *et al.* 2000; Riebel & Smallegange 2003). The results of my study, however, imply that for juvenile Zebra Finches living in a multi-tutor environment, it is less common to learn complete tutor motifs than expected. They appear to learn single syllables instead of motifs, and do not necessarily prefer their fathers (genetic or social) as song tutors.

In the book chapter "In Search of the Song Template", Adret (2004b) states that: "*The auditory template theory – the conversion of memorised song to produced song using feedback as an error-correction mechanism – is central to neurobiological studies of birdsong learning. The essence of the theory is the construction of a complex sound replica based on a set of both genetic and environmental instructions*." This 'complex sound replica' can be defined as the song template. Juvenile birds are supposed to learn this template from an adult tutor and use it as a kind of blueprint for their own song, by means of auditory feedback. It is generally assumed that in many species, the aim of song learning to produce a copy of tutor song (Beecher & Brenowitz 2005; Marler 1970), and Nowicki *et al.* (2002) found that female Song Sparrows preferred males that had learned better in a copulation solicitation assay with songs of laboratory-reared males that differed in the amount of learned versus invented material, although alternative strategies for song learning have been described as well (Beecher & Brenowitz 2005). According to Slater & Lachlan (2003), deviation from the template arises when juveniles add or delete syllables from a song, substitute one syllable for another, or modify an existing syllable in a substantial way. Another possibility is that sequences that were previously only found in two different tutor motifs are recombined to form a new motif (Slater & Lachlan 2003).

Rose et al. (2004) showed that white-crowned sparrows that were tutored with only pairs of normally adjacent syllables were able to assemble motifs in which the syllables were placed in the correct order. This indicates that paired syllables provide the minimal representation of the template necessary for generating complete motifs and correct song structure. This hypothesis is confirmed by the finding that birds that were tutored with reverse-ordered syllable pairs, produced motifs with reversed syllable order. Birds that were tutored with all syllables, but presented singly, failed to produce normal motifs. Since the learning style of white-crowned sparrows is comparable to that of Zebra Finches, it is well possible that these conclusions are transferable to our study.

In my experiment I showed that even birds that learned from more than one tutor mostly had one main tutor. From this tutor, they did not only learn syllables, but also syllable order and, to a lesser extent, temporal structure of the motif. This is generally in line with the conclusions of Slater and Lachlan (2003), who state that if offspring produce a motif that is different from the (main) tutor motif, "*the change involved is relatively minor, fitting in with the notion that copy errors are involved rather than the generation of difference for some functional reason*". However, in some cases the differences found between tutor and offspring motif cannot be defined as "relatively minor": as shown in Chapter 3, some offspring motifs do not resemble any tutor motifs at all. So far, no valid explanation can be given for this phenomenon.

4.5.5 Song Learning: Why?

When considering why offspring birds learn more from certain tutors than others, it cannot be excluded that they just pick the syllables that are easiest to produce and/or learn. This would be in line with the fact that juvenile Zebra Finches raised in acoustic isolation are able to produce song (Derégnaucourt 2011) and that isolate song is also accepted as a valid song model (Williams *et al.* 1993).

Theoretically, it is possible that the observed tutor preference is an artefact of domestication, and juvenile Zebra Finches simply learn the syllables and/or motifs that are easiest to produce, as long as this has no negative effect on overall fitness. Although there is no hard evidence to support this theory (yet), I think it worthwhile to speculate on the implications. In an aviary environment, survival chances are almost equal for all individuals. This probably not only reduces competition over social dominance and the importance of dominance ranks, but could also reduce the motivation for learning complex song. Similar patterns can be expected for example in human students who are obliged to learn a foreign language, but are free to choose which one. As long as the choice is not expected to influence future success, students will tend to choose the language which is easiest to learn. Although for the human example this only seems to be the path of least resistance, it could also be interpreted as efficient in terms of energy. The choice will probably change as soon as the future success varies: students will then be prepared to put more effort in learning a difficult foreign language when it promises more success in the future.

Compared to non-tutors, preferred tutors do not produce motifs that are shorter or contain fewer syllables, and they do not form a homogenous group in terms of song quality. The idea of selection of easy models is therefore unlikely, so if the selection of "easy tutors" might happen, then this needs to be on the level of syllable-selection. Although it is difficult to determine what is "easy" and what is "difficult", indications can be found in the study of Vicario (1991). He found that birds whose syrinx has been denervated unilaterally, or even bilaterally, are still able to produce harmonic stacks, which means that little or no muscles

are involved in producing sounds that at least look rather complex. However, for syllables that include fast frequency modulations as most of the zebra finch syllable do, it is currently unknown if they are easy to produce or not.

Another interesting question is whether juvenile birds at the start of song learning have a fixed idea as to how their own song is supposed to be like once it is crystallised, or whether they gain or lose syllables and motif structure during development. In order to answer these questions, more research is necessary.

4.6 Vocal Interactions and Song Learning (experiment 2)

4.6.1 Communication

Another hypothesis for tutor choice that has not been discussed so far is that juvenile Zebra Finches may learn most from those males with whom they communicate most (Clayton 1987; Eales 1987a). Juvenile Zebra Finches are expected to have most vocal interactions with their fathers and brothers (Roper & Zann 2006), but this does not necessarily have to be the case.

Among group living species, communication is crucial for different aspects of everyday life, like foraging, moving, mating and learning. Although communication is readily associated with vocalisation, it can take place in many different ways. Honeybees communicate the locations of profitable food sources by complex dances, ants coordinate group life through olfactory cues (odours), fireflies use visual signals (light flashes), and many species use pheromones and other chemical cues for signalling (Alcock 1998; Krebs & Davies 1993). In populations of Zebra Finches, communication through vocal interactions seems most important. Vocalisations can convey information about the environment, as well as about the sender identity, physical characteristics, emotional state and motivation. Group life is largely organised through vocalisations (calls) and vocal interactions play a crucial role in the process of song learning (Zann 1996).

4.6.2 The Importance of Calls

In an interesting paper on the effects of corticosterone on Zebra Finch calls, Perez *et al.* (2012) state: "*Within a species, individuals often produce different context-specific types of calls that are characterized by different structures (amplitude, frequency, duration, etc.). These calls generally carry stable characteristics related to the emitter's sex or individual identity, but also more instantaneous information such as the sender's motivation or physiological state*". In Zebra Finches, calls are used for communication within groups and between pair members (Zann 1996). Within pairs, call relations can change over time and are tuned to specific environmental conditions (D'Amelio & Ter Maat, unpublished data). It can be assumed that different Zebra Finch vocalisations have specific meanings, as is the case in various species of social primates (e.g. Vervet monkeys: Seyfarth *et al.* 1980; and Campbell's Monkeys: Zuberbühler 2001) and birds (White-Browed Scrubwren: Leavesley & Magrath 2005; Carrion Crow: Gill & Ramenda, unpublished data; and Black Capped Chickadee: Templeton *et al.* 2005). Understanding the meaning of these calls is an ambitious goal, and even distinguishing between different calls based on acoustic parameters, is difficult. Until recently, Zebra Finch calling behaviour was a relatively underexposed topic, but the tools and techniques described in this thesis offer ample possibilities to further

explore their importance and meaning. Calling could also play an important role in tutor choice, which is an interesting hypothesis that I tested in experiment 2.

4.6.3 Vocal Interactions and Social Behaviour

One of the most striking results of this experiment was that some birds are clearly involved in more vocal interactions than others. The easiest explanation would have been that these birds just vocalise less than others, but investigation of the raw data revealed that this was not the case. Although some birds vocalise significantly less than others, these were not the birds that were involved in least interactions. An alternative explanation would be that some birds are just more social than others, and that sociality can be defined as a personality trait. Recent studies have revealed clear and consistent differences in personality traits like exploratory behaviour, neophobia, etc. (David *et al.* 2011; Dingemanse *et al.* 2002; Dingemanse *et al.* 2004; Schuett *et al.* 2011) and it would be interesting to also test for sociality (as a personality trait) in future experiments.

A third possibility is that the males who are least involved in social interactions with other males interact more with females. This hypothesis cannot be verified with the current data, since the females in our group were not equipped with backpack microphones and the behavioural observations are not sufficient to draw conclusions from. However, this would also be an interesting topic for further research.

Another clear result I obtained is that strongest vocal interactions occurred between offspring birds, especially between siblings. Although this result is not unexpected, it is still interesting. It could for example explain the relatively high rates of syllable sharing among offspring and is in line with predictions by Williams (1990), who found that offspring birds in an aviary keep together in groups that she identified as crèches.

4.6.4 Vocal Interactions and Tutor Choice

The main aim of this study was of course to test if juvenile Zebra Finches learn their song from the adult tutor with whom they have most vocal interactions. I found that some of them interacted more with one tutor than with the other two, but this result was not clearly related to song learning. No clear correlations between adult tutors and offspring were found in February and March, and two birds even interacted most with tutors to whom they were not related in any way. However, it is reasonable to assume that birds do interact more with their tutors than with other adults when they are younger. As described before, this was not done yet due to methodological difficulties and time constraints.

Since I have the sound recordings of all birds from ca. day 25 post hatching, it is possible to test this hypothesis with the current data. However, it is difficult to analyse them since the vocalisations of younger birds are more variable and thus difficult to sort and cluster. Doing so would require the development of more sophisticated methods and tools for analysis: a goal which will be pursued in the near future.

One factor that will probably impede the process of discovering whether offspring birds interact more with their song tutor when they are younger is the feeding behaviour. Juvenile Zebra Finches are fed by their parents until approximately day 35 post hatching (Zann 1996). Both Williams and Reers *et al.* observed that female Zebra Finches only feed their own offspring, but males do not strictly discriminate (Reers *et al.* 2011; Williams 1990). Vocalisations (mostly begging calls) are involved in feeding behaviour as well, which makes it difficult to determine whether the birds interact with an adult as part of the song learning

process, or if they just want to be fed. In order to disentangle this, more research is necessary, where continuous recordings of vocalisations are combined with behavioural observations.

4.6.5 Methodological Considerations

With the methods I presented in Chapter 2, I was able to obtain remarkable results that finally shed some light on the vocal interactions going on in a group of freely behaving Zebra Finches. Despite minor technical difficulties, the tools I used are reliable and relatively easy to use. They offer a wide range of opportunities for studying the social aspect of vocal behaviour and vocal development and can be optimised and/or customised for various experiments. In male Zebra Finches, there are no indications that natural behaviour is impaired by the backpacks. However, the antennae of the current backpacks could cause problems for females during egg-laying and incubation. In order to prevent this, the next generation backpacks have been developed with flexible antennae embedded in the silicon tube, so as to enable even more freedom of movement.

The backpack microphone transmitter system in combination with the multi-channel receiver and recording software can not only be used on Zebra Finches, but on other species as well. Theoretically it is also possible to do experiments with even more individuals that are all freely behaving and interacting in a semi-natural environment.

4.7 Overview and Final Remarks

4.7.1 Alternative Hypotheses to Explain Tutor Choice

So far, I have suggested and tested many hypotheses that could explain tutor preferences, but there are alternatives that deserve some attention here too. One very interesting hypothesis is that juveniles possibly prefer learning from impudent males, who readily interrupt and/or overlap the song of others. In order to test this, continuous recordings of all individuals are necessary. Although these data are available, analysing them requires the development of new methods, which was not possible within the scope of this thesis, but will continue in the near future.

Furthermore, it is possible that juvenile Zebra Finches learn from males that vocalise in close spatial proximity, irrespective of social or aggressive interactions (Jones & Slater 1996; Mann & Slater 1995). The possibility of close proximity, which may require a special "listening" behaviour of the juvenile, as observed in by Houx *et al.* (2000), or a special "tutoring" behaviour of the adult male, has not been investigated yet. The reason therefore is that it is essential to have knowledge of the exact position of all animals throughout the process of song development, i.e. continuous audio AND video recordings, which is still technologically challenging.

4.7.2 Conclusion

The experiments that I described in my thesis have yielded valuable results, but have also been helpful in identifying questions that need to be addressed in future experiments. I explored and proposed many hypotheses that could explain why certain tutors are preferred over others, and I summarised the factors that could influence tutor choice in the diagram below.

total number of surviving offspring		number of syllables per motif		social interaction	
dominance rank		average motif duration		spatial proximity	
body size (mass)		motif stability (similarity score)		singing activity	
pair status (paired/single)		song amplitude (loudness)		song simplicity	
number of extra-pair offspring		song rate (motif repetition)		…… ……	
genetic/social paternity		interrupting song of others			
colour of leg rings					

This diagram gives an overview of all factors that were brought up in this thesis to explain tutor preference. Filled crosses indicate that these hypotheses have been tested and were rejected; open crosses indicate that based on preliminary results, these hypotheses can be rejected; question marks indicate hypotheses that have been proposed, but need to be tested more thoroughly. The diagram leaves room for new hypotheses, since it is possible that alternative hypotheses arise in the future.

In this thesis I focused on the factors that influence the process of song learning and tutor choice in Zebra Finches, and although many questions still remain unanswered, there are also many other exciting aspects of Zebra Finch social behaviour, song learning and vocal communication that need to be explored. Of course it is impossible to answer all of these questions, but it is also a great challenge, and I would like to be a part of it.

Summary

In most species that live in groups, social and vocal interactions play an important role in communication and life in general. Humans, like many species, have the innate ability to produce sound, but using these sounds in a structured way, the way humans do this in speech, is something that needs to be learned. This process of vocal learning is rare in the animal kingdom, but not unique to us: other examples of vocal learners are bats, cetaceans, elephants, hummingbirds, parrots and songbirds. Of these species, birds have probably been investigated most thoroughly, since birdsong and vocal learning are interesting in itself, but also because of the parallels between song learning and speech acquisition in humans.

Zebra Finches (*Taeniopygia guttata*) are often used as model species for studying vocal learning, since they are easy to keep and breed in captivity. The males of this species produce unique song motifs that allow individual recognition, and much is already known about their physiology and behaviour. Male Zebra Finches learn their song motif in early life by imitation of adult tutors. When the birds are ca. 100 days old, the song motif does not change anymore (i.e. song is crystallised). Because of the limited time period in which they can learn their song, Zebra Finches are called “closed-ended learners”.

Zebra Finches are small, highly social and monogamous passerines that roost and breed together in stable colonies and may congregate into larger foraging flocks during daytime, and coordinate group life mainly by means of vocalisations. They are not territorial, but are known to defend their nests. Zebra Finches are opportunistic breeders and both males and females provide parental care. Pair bonds are usually very strong and numbers of extra-pair offspring low. They are native to a wide range of Australia and parts of Indonesia, but are also the third most popular cage birds (after Budgerigars and Canaries).

In my thesis I mainly focus on the factors that influence the process of song learning and tutor choice. Therefore, I investigate the role of social environment, physiology and song characteristics. An important finding is that my study animals clearly and consistently learn more from certain song tutors than from others. These preferred tutors may be genetically unrelated and I discuss several hypotheses that could explain these preferences.

Since Zebra Finches live in groups, population density could be an important factor in determining the social environment. In the wild, population density locally increases when conditions are harsher and resources (like food and water) get scarce, but so far relatively little is known about the effects of population density on development and reproduction. Studying density effects on physiology and behaviour might also be helpful in identifying optimal group size, which would help to optimize Zebra Finch wellbeing in captivity.

I investigated the possible effects of population density in four aviaries with different density levels (2 high and 2 low), with 10 male and 10 female Zebra Finches per aviary. I found that birds in lower density conditions produced more and larger (body mass, tarsus length) surviving offspring than birds in high density conditions. Furthermore, offspring in low density aviaries produced slightly longer song motifs and more different syllables than their tutors, whereas offspring in high density aviaries produced shorter motifs and a smaller or similar number of different syllables than their tutors. Aggression levels within the populations were low throughout the experiment, but the number of aggressive interactions was significantly higher in high density aviaries.

Regarding population density, I also measured baseline plasma corticosterone (stress hormone) levels and found that these were generally low in all four experimental aviaries. Population density did not seem to have an effect, indicating that even the high density conditions did not cause extreme stress to the birds. On day 15 post hatching, brood size and baseline corticosterone levels were positively correlated. On days 60 and 100 post hatching this correlation was no longer present.

The results of this experiment prove that population density affects various aspects of Zebra Finch life and development, with birds living in low population density conditions having an advantage over those living under higher population density conditions.

It is known that within groups of captive Zebra Finches, some individuals are consistently more dominant than others. Social dominance, defined as consistently winning agonistic interactions (Drews 1993), is often associated with increased reproductive success, since dominant individuals usually gain priority access to resources like territories, food, water and mates. Although differences in dominance status have been observed, not much is known about predictors of dominance.

In my experiments I derived social dominance from spontaneous agonistic interactions and found clear but not strictly linear patterns. Dominance ranks were compared with average perching position, physiological traits and reproductive success for all individuals. Positive correlations were found between behavioural rank and perching position (more dominant birds occupied higher perching positions) and behavioural rank and body size (bigger birds were more dominant). Dominance did not correlate with song complexity (number of syllables per motif and motif duration), reproductive success and baseline plasma corticosterone levels. However, an interesting trend was found towards lower song complexity (less syllables per motif, shorter motif duration) in bigger birds.

It is possible that dominance hierarchies are not that strict in captive conditions, since being dominant does not offer big advantages when resources are plenty, but become more important when conditions get harsher. A possible explanation for the lack of strong dominance patterns in my study populations therefore is that my birds did not have to compete over resources. In this case, dominance patterns probably only serve as a means to facilitate group life and reduce numbers of agonistic interactions. I tested whether juvenile Zebra Finches preferred more dominant males as song tutors, but did not find any correlation.

Although Zebra Finches are monogamous birds that usually form strong pair bonds both in the wild and in captivity, extra pair copulations (EPC) resulting in extra pair offspring (EPO) are not uncommon. What is interesting is that numbers of EPO found in captive populations are much higher than in the wild. This may be due to effects of confinement and domestication, differences in the intensity of mate guarding, or the existence of different reproductive strategies.

In my first experiment, I monitored behaviour and reproductive success of the adult Zebra Finches and found an overall EPO rate of 16.5%, as well as individual differences in reproductive and behaviour patterns. I divided these patterns into five categories: 1) monogamous pair *with* offspring, *without* EPO; 2) monogamous pair *with* offspring, *with* EPO; 3) monogamous pair *without* offspring; 4) single *with* EPO; 5) single *without* offspring. No gender differences were found, but there were significant differences in reproductive

success between categories, with birds from category 2 being most successful. This pattern was the same in each aviary.

It is possible that the different categories I defined really represent different (genetically determined) reproductive strategies, which are adaptive to specific environmental conditions. If so, maintaining a monogamous pair bond AND engaging in extra-pair copulations may be the optimal strategy in an aviary environment. However, more research is necessary in order to draw any real conclusions. Based on the results of my study it cannot be excluded that more birds engaged in EPC as expected based on numbers of EPO. Therefore, it is essential to continue studying this topic in order to define whether the observed behavioural and reproductive patterns really represent different reproductive strategies in Zebra Finches.

I investigated whether the tutor preferences of juvenile Zebra Finches were correlated to the reproductive success of the tutor, number of extra-pair offspring or pair status (single/paired), but again did not find any relationships.

One of the main aims of my thesis was to find out whether juvenile Zebra Finches growing up in a more natural situation with many potential song tutors still prefer their father's song, or rather learn their song from other tutors. I provide a literature background and analysed the songs recordings of the young Zebra Finches from my experimental aviaries with several methods. I found that these birds learned song syllables rather than complete song motifs and that these syllables could be categorized into (1) real copies of tutor syllables; (2) imitations of tutor syllables; (3) variations on tutor syllables; (4) elements of tutor syllables; or (5) new syllables. I listed category 4 as a separate category because juvenile Zebra Finches occasionally do not learn complete syllables but only parts, which they may recombine with other parts. This category contains imitations and variations on parts (elements) of tutor syllables.

As mentioned before, I also found clear preferences for certain adult tutors, with several offspring sharing a preference for the same tutor. Interestingly, the preferred tutors were not necessarily the (genetic and/or social) fathers, the males with the highest reproductive success (number of offspring), the biggest, or the most dominant males. Some adult males were never learned from, although these males did not differ in any way (body size, behaviour, song quality) from the others.

For one aviary, I investigated whether tutor choice was related to song characteristics of all potential tutors, but did not find any clue here either. I did find, however, that many juveniles learned pieces of song from more than one adult male, although most of them had one main tutor. The birds that learned from only one tutor seemed to have more stable song than those who learned from more than one tutor.

I also pose the question whether juvenile Zebra Finches really choose a tutor; or rather choose a convenient song model, and discuss how my results fit into the theory of song template learning. Finally, I conclude that although many of our offspring birds learned from more than one tutor, most (but not all) had one main tutor from whom they not only learned syllables, but also syllable order and temporal structure of the motif. This can be interpreted as an indication for template learning.

Since all of the initial hypotheses I tested failed to explain tutor preferences, I tried another approach. All bird species, including Zebra Finches, are capable of vocal communication by

means of calls, without ever having been into contact with adult conspecifics. However, some male vocalisations (song, distance calls) are acquired through social learning.

In my second experiment I started to test the hypothesis that juvenile Zebra Finches may learn more from song tutors with whom they have most vocal interactions. For this purpose, I made continuous and simultaneous recordings of all individual male group members (>25 days post hatching) in a semi-natural environment, using backpack microphone transmitters. This is a completely new procedure, which is why carrying out the study and analysing the data was challenging. I therefore present preliminary data of birds >day 65 post hatching, since vocalisations are clear enough to analyse with the current methods.

Intuitively the tutors with whom juveniles interact most would be the fathers, but especially in larger colonies, this is not necessarily the case. I found that some birds were involved in more interactions than others, although they did not differ in the total amount of vocalisations. Most and strongest vocal interactions occurred between offspring birds, especially between siblings.

For the days that have been tested so far, less strong interactions occurred between offspring and tutors and I was not able to identify a correlation between vocal interactions and tutor choice. However, it is possible that juveniles learn from tutors with whom they have most vocal interactions during earlier stages of development. I was not able to test this within the scope of this thesis, because vocalisations of younger birds are less clear and analysis requires further development of the current methods.

I discuss the general insights I gained through this study in a broader theoretical framework, and although my experiments took place under controlled laboratory conditions, some careful extrapolations could be made, which allow statements about Zebra Finches in general. The experiments I describe in my thesis have yielded valuable results, but some questions remain unanswered and some hypotheses are still to be tested. Therefore, I also give an outline for future research in the final chapter.

Zusammenfassung

Bei den meisten Arten die in Gruppen leben, spielen vokale Interaktonen eine wichtige Rolle in der Kommunikation und im Alltag im Allgemeinen. Wie viele Arten haben Menschen die angeborene Fähigkeit Töne zu produzieren, aber die Möglichkeit diese strukturiert einzusetzen, sowie in Sprache, will gelernt sein. Dieser Prozess des vokalen Lernens ist selten im Tierreich, aber nicht einzigartig für den Menschen: andere Beispiele vokaler Lerner sind Fledermäuse, Delfine und Elefanten, Kolibris, Papageien und Singvögel. Die am besten erforschte Gruppe ist wohl die der Singvögel, weil Gesangslernen an sich sehr interessant ist, aber auch wegen der Parallelen zum Spracherwerb bei Menschen.

Zebrafinken (*Taeniopygia guttata*) werden oft als Modell benutzt um vokales Lernen zu studieren, weil sie sich leicht in Gefangenschaft halten und züchten lassen. Die Männchen dieser Art produzieren einzigartige Gesangsmotive, aufgrund dessen man sie individuell erkennen kann, und es ist schon viel bekannt über die Physiologie und das Verhalten. Männliche Zebrafinken lernen ihr Gesangsmotiv am Anfang ihres Lebens indem sie erwachsene Tutoren nachahmen. Wenn sie ca. 100 Tage alt sind, verändert sich das Gesangsmotiv nicht mehr und man bezeichnet den Gesang als “kristallisiert”.

Zebrafinken sind kleine, sehr soziale und monogame Singvögel, die in stabile Kolonien nächtigen und brüten. Tagsüber können Kolonien zur Futtersuche in großen Schwärmen zusammenkommen. Das Leben in der Gruppe wird hauptsächlich über Vokalisationen koordiniert. Zebrafinken sind nicht territorial, aber bekannt dafür ihre Nester zu verteidigen. Sie brüten opportunistisch und sowohl die Männchen als die Weibchen versorgen die Jungen. Die Paarbindung ist generell sehr stark und die Zahl der außer-Paar Nachkommen gering. Zebrafinken sind in großen Teilen Australien und ein Teil Indonesiens beheimatet, aber auch die drittbeliebtesten Käfigvögel (nach Wellensittiche und Kanarienvögel).

In meiner Dissertation konzentriere ich mich auf die Faktoren, die den Prozess des Gesangslernens und die Wahl der Tutoren beeinflussen. Hierzu erforsche ich die Rolle des sozialen Umfeldes, der Physiologie und der Gesangsmerkmale. Eine wichtige Erkenntnis zu der ich gekommen bin, ist dass meine Tiere eindeutig und konsequent mehr von bestimmten Tutoren lernen als von Anderen. Mit diesen “bevorzugten Tutoren” müssen sie nicht unbedingt verwandt sein, und ich diskutiere einige Hypothesen die diesen Präferenz erklären könnten.

Weil Zebrafinken in Gruppen leben, könnte Populationsdichte ein wichtiger Faktor sein bei der Bestimmung des sozialen Umfeldes. In freier Wildbahn nimmt die Populationsdichte örtlich zu wenn die Bedingungen schwerer werden und Ressourcen wie Nahrung und Wasser knapp werden. Bislang ist aber wenig bekannt über die Auswirkungen auf die Entwicklung und Fortpflanzung. Die Effekte der Populationsdichte auf Physiologie und Verhalten zu studieren, könnte hilfreich sein beim Feststellen der optimalen Gruppengröße, was dem Wohlbefinden der Zebrafinken in Gefangenschaft zu Gute kommen könnte.

In vier Volieren mit unterschiedlicher Populationsdichte (2 hoch, 2 niedrig) und 10 Männchen und 10 Weibchen pro Voliere, habe die mögliche Dichte-Effekte erforscht. Ich habe festgestellt, dass Vögel, die bei niedrigerer Populationsdichte gehalten werden, mehr und größere Nachkommen produzieren. Außerdem singt der männliche Nachwuchs bei niedrigerer Populationsdichte längere Lieder, die auch aus mehr unterschiedlichen Silben aufgebaut sind als bei ihren Tutoren. Bei höherer Populationsdichte sind die Lieder kürzer und sind aus weniger Silben aufgebaut. Während des ganzen Versuchs gab es relativ wenig Aggressivität, aber die Zahl der aggressiven Interaktionen war signifikant höher in den Volieren mit höherer Populationsdichte.

Bezüglich Populationsdichte habe ich auch die Basis-Kortikosteron (Stress-Hormon) Werte im Blutplasma gemessen und festgestellt, dass sie generell in allen Volieren niedrig waren. Populationsdichte schien kein Effekt zu haben, ein Hinweis dass sogar die hohe Populationsdichte in meinem Versuch zu keinen allzu großen Sress für die Tiere geführt hat. Am Tag 15 nach Schlüpfen gab es eine positive Korrelation zwischen Brutgröße und Kortikosteron-Werte, aber am Tag 60 und 100 nach Schlüpfen war eine solche Korrelation nicht mehr nachzuweisen.

Die Ergebnisse dieses Versuchs zeigen, dass Populationsdichte ein Effekt hat auf unterschiedliche Aspekte des Lebens und die Entwicklung von Zebrafinken. Vögel, die in niedrigerer Populationsdichte leben haben dabei einen Vorteil gegenüber jenen, die in höherer Populationsdichte leben.

Es ist bekannt, dass manche Individuen in Gruppen von Zebrafinken in Gefangenschaft konsequent dominanter sind als andere. Soziale Dominanz, definiert als das konsequenter Gewinnen agonistischer Interaktionen, wird

oft mit erhöhtem Fortpflanzungserfolg assoziiert, weil dominante Individuen generell ein Vorteil haben bei der Exploitation verschiedener Ressourcen, wie geeignete Territorien, Nahrung, Wasser und Partner. Obwohl es Unterschiede im Dominanz-Status gibt, ist relativ unklar von welchen Faktoren Dominanz bestimmt wird. In meinen Versuchen habe ich soziale Dominanz abgeleitet von spontanen agonistischen Interaktionen, und habe klare, aber nicht strikt lineare Muster gefunden.

Für jedes Individuum wurde die Position in der Dominanz-Hierarchie verglichen mit der Sitzposition, physiologischen Merkmale und Fortpflanzungserfolg. Die Position in der Hierarchie war positiv korreliert zur Sitzposition (dominantere Tiere sitzen oben) und Körpergewicht (schwere Vögel sind dominanter). Es gab keine Korrelation zu Gesangsqualität, Fortpflanzungserfolg und Kortikosteron (Stress-Hormon), aber es gab einige interessante Trends: es scheint z.B. so zu sein dass größere Vögel kürzere und weniger komplexe Lieder singen.

Es ist möglich, dass Dominanz-Hierarchien bei Zebrafinken in Gefangenschaft nicht so fest und wichtig sind, weil es nicht direkt von Vorteil ist dominant zu sein, wenn es keine oder kaum Konkurrenz gibt, um z.B. Nahrung, Wasser oder Nistgelegenheit. Wenn die Bedingungen ungünstiger werden, kann sich die Situation aber ändern. Eine mögliche Erklärung für die Abwesenheit starker Dominanzmuster in meinen Volieren ist, dass meine Vögel nicht um Ressourcen konkurrieren mussten. In diesem Fall ist die wichtigste Funktion der Dominanz-Struktur wahrscheinlich die Vereinfachung des sozialen Lebens und das geringer werden der Zahl der agonistische Interaktionen. Ich habe überprüft ob junge Zebrafinken dominante Männchen als Gesangstutor bevorzugen, aber dies schien nicht der Fall zu sein.

Obwohl Zebrafinken monogame Vögel sind, die starke Paarbindungen formen, sowohl in Gefangenschaft als in freier Wildbahn, sind außer-Paar Paarungen (APP) und daraus fortkommende außer-Paar Nachwuchs (APN) auch keine Seltenheit. Interessant ist, dass es in Gefangenschaft viel mehr APN gibt als in freier Wildbahn. Es ist möglich, dass dies vom Leben in Gefangenschaft oder durch Domestizierung verursacht worden ist, oder von der Intensität mit der die Tiere ihre Partner beschützen, oder von der Existenz unterschiedlicher Fortpflanzungsstrategien.

In meinem ersten Versuch habe ich Verhalten und Fortpflanzung der erwachsenen Zebrafinken beobachtet und eine totale APN-Rate von 16.5%, als auch individuelle Unterschiede in Fortpflanzungs- und Verhaltensmuster gefunden,. Diese Muster habe ich in 5 Kategorien untergebracht: 1) monogam mit Nachwuchs, ohne APN; 2) monogam mit Nachwuchs, mit APN; 3) monogam ohne Nachwuchs; 4) single mit APN; 5) single ohne Nachwuchs. Es gab keine geschlechts-bedingten Unterschiede, aber es wurden signifikante Fortpflanzungserfolgsunterschiede gefunden zwischen den unterschiedlichen Kategorien. Vögel aus Kategorie 2 waren dabei am erfolgreichsten. Dieses Muster war gleich in allen Volieren.

Es ist möglich, dass die unterschiedlichen Kategorien, die ich definiert habe, unterschiedliche (genetisch festgelegte) Fortpflanzungsstrategien representieren, die adaptiv sind für spezifische Umweltbedingungen. Wenn dies der Fall ist, kann es sein dass es in einer Volieren-Umgebung optimal ist monogam zu sein UND fremdzugehen. Aufgrund der Ergebnisse dieser Studie kann auch nicht ausgeschlossen werden, dass mehr Vögel fremdgehen als erwartet aufgrund der Zahl der APN. Es ist deshalb erforderlich weiterzuforschen damit festgestellt werden kann, ob die bei Zebrafinken beobachteten Verhaltens- und Fortpflanzungsmuster tatsächlich unterschiedliche Fortpflanzungsstrategien representieren.

Ich habe untersucht ob die Tutorpräferenzen der Jungtiere mit dem Fortpflanzungserfolg, Zahl der Außer-Paar Nachkommen oder dem Paar-Status (single/verpaart) korreliert war, konnte aber keine Zusammenhänge finden.

Eins der Hauptziele meines Projekts war herauszufinden ob junge Zebrafinken, die in einer eher natürlichen Situation mit vielen potenziellen Tutoren aufwachsen, immer noch ihre Väter als Gesangstutor bevorzugen oder ihr Lied lieber von anderen Tutoren lernen. Ich biete einen theoretischen Hintergrund und beschreibe wie die Gesangsmotive der erwachsenen und jungen Männchen aus meinen Versuchen analysiert worden sind. Ich habe festgestellt, dass die Vögel eher einzelne Silben als komplette Motive lernen, und die Silben konnten in 5 Kategorien eingeteilt werden: (1) Kopie; (2) Imitation; (3) Variation; (4) Element; oder (5) neue Silbe. Kategorie 4 habe ich separat aufgeführt weil junge Zebrafinken manchmal nicht eine komplette Silbe, sondern nur Teile davon lernen, die sie beliebig kombinieren können. Diese Kategorie enthält Imitationen und Variationen von Teilen (Elemente) der Tutor-Silben.

Wie vorher schon erwähnt, habe ich festgestellt, dass die Jungtiere klare Preferenzen für bestimmte Tutoren haben, und diese auch untereinander teilen. Interessanterweise waren die beliebtesten Tutoren aber nicht unbedingt die (genetischen und/oder sozialen) Väter, Männchen mit dem größten Fortpflanzungserfolg (Zahl

der Nachkommen), die größten oder die dominantesten Männchen. Von manchen Männchen wird nie gelernt, obwohl sie sich in keinerlei Weise (Körpergröße, Verhalten, Gesangsqualität) von den anderen unterscheiden.

In einer Voliere habe ich untersucht, ob Tutorpräferenzen mit den Gesangsmerkmalen der potenziellen Tutoren zusammenhängen, aber auch hier gab es keine Verbände. Ich habe allerdings festgestellt, dass viele Jungtiere Teile des Gesangs unterschiedlicher Tutoren gelernt haben, obwohl die meisten einen "Haupt-Tutor" hatten. Die Vögel, die nur von einem Tutor gelernt hatten, produzierten stabilere Gesangsmotive als die, die von mehreren Tutoren gelernt hatten.

Ich stelle die Frage, ob junge Zebrafinken einen Tutor oder eher ein passendes Gesangsmodell auswählen und im Hinblick auf die "Template-Theorie" gehe ich davon aus, dass die meiste Jungtiere einen "Haupt-Tutor" haben, obwohl viele von mehreren Tutoren lernen. Vom Haupt-Tutor lernen die Jungen nicht nur Silben, sondern auch die Reihenfolge und zeitliche Struktur des motivs . Dies kann als Indiz für "Template-Lernen" interpretiert werden.

Da keine der Hypothesen die beobachtete Tutorpräferenz erklären konnte, habe ich einen anderen Ansatz überprüft. Alle Vogelarten, Zebrafinken inklusive, sind in der Lage über Vokalisationen zu kommunizieren. Kontakt zu erwachsenen Artgenossen ist dazu nicht zwingend erforderlich. Manche männliche Vokalisationen (Gesang, Kontakt-Rufe) müssen jedoch in einer sozialen Umgebung gelernt werden.

In meinem zweiten Experiment habe ich angefangen zu untersuchen, ob junge Zebrafinken wohlmöglich am meisten von den Tutoren lernen, mit denen die häufigsten vokalen Interaktionen stattfinden. Hierzu habe ich von allen männlichen Gruppenmitglieder (>25 Tage nach Schlüpfen) mit Hilfe von Rucksack-Mikrophonsender in einer semi-natürlichen Umgebung kontinuierliche und simultane Tonaufnahmen gemacht. Da dies ein komplett neues Verfahren ist, war es eine Herausforderung, diese Studie durchzuführen und die Ergebnisse auszuwerten. Ich stelle hier deshalb nur die Daten von Vögeln >65 Tage nach Schlüpfen vor, weil ihre Vokalisationen klar genug sind, um sie mit den jetzigen Methoden auszuwerten.

Intuitiv würde man davon ausgehen, dass die Jungtiere die meisten Interaktionen mit ihren Vätern haben, aber vor allem in größeren Kolonien ist dies nicht unbedingt der Fall. Ich habe festgestellt, dass manche Vögel in mehr Interaktionen involviert sind als andere, obwohl es keine Unterschiede in der Zahl der Vokalisationen gibt. Die häufigsten und am stärksten ausgeprägten Interaktionen haben zwischen Jungtieren, insbesondere zwischen Brüdern, stattgefunden.

Während der bis jetzt ausgewerteten Tage habe ich nur schwächere Interaktionen zwischen Nachwuchs und Tutoren gefunden, Korrelationen zwischen vokalen Interaktionen und Tutorpräferenz konnte ich jedoch nicht feststellen. Es ist aber möglich, dass solche Korrelationen in früheren Entwicklungsstadien vorkommen. Im Rahmen meiner Doktorarbeit konnte ich diese Hypothese noch nicht überprüfen, da die Vokalisationen jungerer Vögel weniger klar sind, und die jetzigen Analysemethoden dafür erst weiterentwickelt werden müssen.

Das allgemeine Verständnis, das ich während meiner Doktorarbeit erlangt habe, bewegt sich in einem breiten theoretischen Rahmen. Obwohl meine Versuche unter kontrollierte Bedingungen stattgefunden haben, ist es doch möglich, vorsichtige Extrapolationen zu machen und Aussagen über Zebrafinken im Allgemeinen zu treffen. Die in meiner Dissertation beschriebenen Versuche haben wertvolle Ergebnisse hervorgebracht, aber manche Fragen sind noch offen und manche Hypothesen noch nicht überprüft. In dem letzten Kapitel gebe ich deshalb auch einige Vorschläge für weitere Forschungsansätze.

Samenvatting

Bij de meeste soorten die in groepen leven, spelen sociale en vocale interacties een belangrijke rol in communicatie, en in het dagelijks leven in het algemeen. Zoals vele soorten hebben mensen de aangeboren vaardigheid geluid te produceren, maar de mogelijkheid om dit geluid gestructureerd te kunnen gebruiken, zoals mensen dat doen in spraak, is aangleerd. Dit proces van vocaal leren is zeldzaam in het dierenrijk, maar niet uniek: andere voorbeelden van dieren die hun "taal" (vocalisaties) moeten leren zijn vleermuizen, dolfijnen en robben, colibri's, papegaaien en zangvogels. Van deze soorten zijn de vogels waarschijnlijk het best onderzocht, omdat vogelzang op zich interessant is, maar ook vanwege de overeenkomsten tussen zang leren bij vogels en spraak leren bij mensen.

Zebravinken (*Taeniopygia guttata*) worden vaak gebruikt als model-soort om vocaal leren te bestuderen, omdat ze eenvoudig te houden zijn en zich ook in gevangenschap makkelijk voortplanten. De mannetjes van deze soort produceren unieke zang-motieven, op grond waarvan ze individueel te herkennen zijn. Bovendien is al veel bekend over het gedrag en de fysiologie. Mannelijke zebravinken leren hun zang-motief aan het begin van hun leven door middel van imitatie van volwassen tutoren. Als ze ca. 100 dagen oud zijn verandert het motief niet meer en spreekt man van uitgekristalliseerde zang.

Zebravinken zijn kleine, zeer sociale en monogame zangvogels, die in stabiele kolonies overnachten en broeden. Overdag kunnen kolonies bij elkaar komen in grote zwermen om samen te foerageren. Hun groepsleven coördineren ze hoofdzakelijk via vocalisaties. Ze zijn niet territoriaal, maar staan erom bekend hun nesten te verdedigen. Zebravinken broeden zodra de omstandigheden het toelaten (onafhankelijk van de jaargetijden) en zowel de mannetjes als de vrouwtjes zorgen voor de kinderen. De paar-band is over het algemeen erg sterk en het aantal buiten-paar nakomelingen laag. Zebravinken komen in grote delen van Australië, en in een deel van Indonesië in het wild voor, maar ze zijn ook de op twee na meest geliefde volièrevogels (na grasparkieten en kanaries).

In mijn proefschrift ga ik vooral in op de factoren die het proces van zang-leren en tutorkeuze beïnvloeden. Hiervoor onderzoek ik de rol van sociale omgeving, fysiologie en de kenmerken van de zang. Een belangrijke ontdekking die ik gedaan heb, is dat mijn dieren duidelijk en consequent meer van bepaalde tutoren leren dan van anderen. Met deze "voorkeurs-tutoren" hoeven ze niet perse verwant te zijn en ik bespreek een aantal hypotheses die de voorkeuren zouden kunnen verklaren.

Omdat Zebravinken in groepen leven, kan populatiedichtheid een belangrijke factor zijn bij de bepaling van de sociale omgeving. In het wild neemt de populatiedichtheid lokaal toe als de omstandigheden slechter worden en hulpbronnen zoals voedsel en water schaars zijn, maar er is weinig bekend over de effecten van populatiedichtheid op ontwikkeling en voortplanting. Het bestuderen van dichtheidseffecten op fysiologie en gedrag kan bovendien nuttig zijn om uit te vinden wat de optimale groepsgrootte is, wat uiteindelijk kan helpen bij de optimalisatie van het welzijn van zebravinken in gevangenschap.

Ik heb de mogelijke effecten van populatiedichtheid getest in vier volières met verschillende dichtheidsniveaus (2 hoog en 2 laag), met 10 mannetjes en 10 vrouwtjes per volière. Ik heb ontdekt dat de vogels bij lagere dichtheid meer en grotere (lichaamsgewicht, tarsuslengte) overlevende nakomelingen produceren dan vogels bij hoge dichtheid. Bovendien produceren de nakomelingen in volières met lagere dichtheid iets langere zangmotieven met meer syllaben zongen dan hun tutoren, waar nakomelingen uit volières met hoge dichtheid kortere motieven zingen met een vergelijkbaar of kleiner aantal syllaben dan hun tutoren. Het agressieniveau in de populaties was laag gedurende het experiment, maar het aantal agressieve interacties was significant hoger in volières met hoge dichtheid.

Met betrekking tot populatiedichtheid heb ik ook baseline corticosteron (stress-hormoon) waardes in het bloed-plasma gemeten. Populatiedichtheid leek geen effect the hebben, wat erop wijst dat zelfs de omstandigheden in de volières met hoge dichtheid geen extreme stress veroorzaakten. Op dag 15 na het uitkomen bestond een positieve correlatie tussen nestgrootte en corticosteron-waarden. Op dag 60 en 100 na het uitkomen kon een dergelijke correlatie niet meer aangetoond worden.

De resultaten van dit experiment tonen aan dat populatiedichtheid effect heeft op verschillende aspecten van het leven en de ontwikkeling van Zebravinken, waarbij vogels die bij lage populatiedichtheid leven een voordeel hebben ten opzichte van vogels in omstandigheden met hoge populatiedichtheden.

Het is bekend dat sommige individuen consequent dominanter zijn dan anderen binnen groepen van zebravinken in gevangenschap. Sociale dominantie, gedefinieerd als het consequent winnen van agonistische

interacties, wordt vaak geassocieerd met verhoogd reproductief succes, omdat dominante individuen over het algemeen het eerste toegang hebben tot bijvoorbeeld geschikte territoria, voedsel, water en partners. Hoewel verschillen in dominantiestatus bekend zijn, is er niet veel bekend over de factoren die bepalen of een individu dominant wordt of niet.

In mijn experimenten heb ik sociale dominantie afgeleid van spontane agonistische interacties en duidelijke maar niet persé lineaire structuren gevonden. Deze werden voor alle individuen vergeleken met de gemiddelde zithoogte, fysiologische kenmerken en het voortplantingssucces. De positie in de dominantie-hiërarchie gebaseerd op gedrags-observaties bleek positief gecorreleerd met gemiddelde zithoogte (dominantere dieren zitten hoger) en met lichaamsgewicht (zwaardere vogels zijn dominanter). Dominantie was niet gecorreleerd met zangcomplexiteit (aantal syllabes per motief en motiefduur), voortplantingssucces en baseline plasma kortikosteron. Ik heb echter een interessante trend gevonden naar lagere zangcomplexiteit (minder syllables per motief, kortere motieven) bij grotere vogels.

Een mogelijke verklaring voor de afwezigheid van sterkere dominantie-patronen in mijn volières is dat dominantie waarschijnlijk belangrijker wordt naarmate de omstandigheden slechter worden, terwijl mijn vogels niet hoefden te concurreren om hulpbronnen. In dit geval dienen dominantie- hiërarchiën waarschijnlijk voornamelijk ter vereenvoudiging van het sociale leven en beperking van het anantal agonistische interacties. Ik heb gekeken of jonge zebravinken een voorkeur hadden voor dominante mannetjes als zang-tutor, maar dit leek niet zo te zijn.

Hoewel Zebravinken monogame vogels zijn die normal gesproken zowel in het wild als in gevangeschap sterke paarbanden hebben, zijn buiten-paar paringen (BPP) die in buiten-paar nakomelingen (BPN) resulteren niet ongebruikelijk.

Wat opvalt is dat het aantal BPN in gevangenschap veel hoger is dan in het wild. Dit kan een gevolg zijn van het leven in gevangenschap of van domesticatie, verschillen in intensiteit van partnerbescherming, of het bestaan van verschillende voortplantings-strategiën.

In mijn eerste experiment heb ik het voortplantingsssucces van de volwassen Zebravinken bestudeerd. Het totaal percentage BPN lag bij 16.5% en ik heb individuele verschillen in voortplantings- en gedragspatronen gevonden. Deze verschillende patronen heb ik in 5 categoriën ingedeeld: 1) monogaam paar met nakomelingen, zonder BPN; 2) monogaam paar met nakomelingen, met BPN; 3) monogaam paar zonder nakomelingen; 4) alleenstaande met nakomelingen; 5) alleenstaande zonder nakomelingen. Ik heb geen verschillen gevonden tussen mannetjes en vrouwtjes, maar er waren significante verschillen in voortplantings-succes tussen de categoriën, waarbij vogels uit categorie 2 in alle volières het meest succesvol waren.

Het is mogelijk dat deze verschillende categorieën ook voor verschillende (genetisch vastgelegde) voortplantingsstrategieën staan, die aangepast zijn aan specifieke omgevingsomstandigheden. Als dat zo is, dan is het onderhouden van een monogame relatie EN vreemdgaan waarschijnlijk de optimale strategie binnen een volière. Er is echter meer onderzoek nodig om definitieve conclusies te trekken. Op grond van de huidige resultaten kan niet uitgesloten worden dat er meer vogels vreemdgaan dan te verwachten is afgaande op het aantal BPN. Het is daarom noodzakelijk meer onderzoek te doen om te kunnen bevestigen of de verschillende voortplantings- en gedragspatronen die in Zebravinken voorkomen ook echt afspiegelingen zijn van verschillende adaptieve voortplantingsstrategieën.

Ik heb onderzocht of de voorkeur voor bepaalde tutoren samenhangt met het voortplantingssucces, het aantal buiten-paar nakomelingen of de status (single/gepaard) van de tutor, maar opnieuw geen verbanden gevonden.

Een van de belangrijkste doelen van mijn promotie-onderzoek was uit te vinden of jonge Zebravinken die in en meer natuurlijke omgeving met meerdere potentiële tutoren opgroeien nog steeds bij voorkeur het lied van hun vader leren, of liever van andere tutoren. Ik bied een theoretische achtergrond en beschrijf hoe de zang-motieven van alle volwassen en jonge mannetjes uit mijn onderzoekspopulaties met verschillende methoden geanalyseerd zijn.

Ik heb vastgesteld dat de vogels vooral enkele syllaben leren in plaats van complete motieven, en dat de syllaben in 5 categoriën ingedeeld kunnen worden: (1) kopie; (2) imitatie; (3) variatie; (4) element; of (5) nieuwe syllabe. Categorie 4 is een aparte categorie omdat jonge Zebravinken soms niet een hele syllabe, maar alleen delen ervan leren, die ze dan naar believen kunnen combineren. Deze categorie bevat imitaties en variaties op delen (elementen) van tutor-syllaben.

Zoals gezegd heb ik ook duidelijke voorkeuren voor bepaalde tutoren gevonden, waarbij meerdere jonge dieren hun voorkeur voor dezelfde tutor delen. Interessant is dat de jongen uit mijn onderzoekspopulaties geen voorkeur hadden voor hun (genetische/sociale) vaders, de mannetjes met het

grootste voortplantingssucces (aantal nakomelingen), of de grootste of meest dominante mannetjes. Van sommige mannetjes werd helemaal niks geleerd, hoewel deze dieren op geen enkele wijze (lichaamsgrootte, gedrag, gezangskwaliteit) van de anderen afwijken.

Voor één volière heb ik getest of tutorkeuze gerelateerd was aan de kenmerken van de zang van alle mogelijke tutoren, maar ook hier heb ik niets ontdekt. Ik heb echter wel vastgesteld, dat veel jongen stukjes van de zang van meer dan een tutor leerden, hoewel de meesten wel een "hoofd-tutor" hadden. De vogels die slechts van een tutor geleerd hadden, leken stabielere zang-motieven te produceren dan degenen die van meerdere tutoren geleerd hadden.

Ook stel ik de vraag of jonge Zebravinken een tutor kiezen, of meer een makkelijk gezangsmodel, en bespreek mijn resultaten in het kader van de "template-theorie". Ik kom tot de conclusie dat hoewel veel vogels van meer dan een tutor leren, de meeste toch een "hoofdtutor" hebben, van wie ze niet alleen syllaben maar ook de volgorde en temporele structuur van het motief. Dit kan uitgelegd worden als een indicatie voor "template-leren".

Omdat geen van de hypotheses die ik getest heb de voorkeur voor bepaalde tutoren kon verklaren, heb ik ook een andere benadering getest. Alle vogels, inclusief Zebravinken, zijn in staat te communiceren door middel van vocalisaties. Hiervoor is het niet noodzakelijk dat ze ooit contact hebben gehad met volwassen soortgenoten. Sommige manneklijke vocalisaties (zang, contact-roep) moeten echter in een sociale omgeving geleerd worden.

In mijn tweede experiment ben ik begonnen de hypothese te testen dat jonge Zebravinken misschien het meeste leren van tutoren met wie ze de meeste interacties hebben. Hiervoor heb ik continue en simultane geluidsopnames van alle mannelijke groepsleden (>25 dagen na uitkomen) in een semi-natuurlijke omgeving gemaakt, met behulp van rugzak-microfoonzenders. Omdat dit een geheel nieuwe procedure is, was het een uitdaging deze studie uit te voeren en de data uit te werken. Ik presenteer daarom alleen de gegevens van vogels vanaf dag 65 na uitkomen, omdat hun vocalisaties duidelijk genoeg zijn om met de huidige methoden te analyseren.

Intuïtief gaat men ervan uit dat jonge vogels het meeste interactie hebben met hun vaders, maar vooral in grotere kolonies is dit niet per definitie het geval. Ik heb ontdekt dat sommige vogels in meer interacties met andere mannetjes betrokken zijn dan anderen, hoewel ze niet meer vocaliseren. De sterkste vocale interacties vonden plaats tussen jonge dieren (vooral tussen broertjes).

Op de dagen die ik tot nu toe uitgewerkt heb waren de interacties tussen jonge dieren en tutoren minder sterk en ik heb geen verband gevonden tussen vocale interacties en tutorkeuze. Het is echter mogelijk dat jonge dieren van die tutoren leren, met wie ze de meeste interactie hebben gedurende vroegere ontwikkelingsstadia. Deze hypothese heb ik in het kader van mijn promotie-onderzoek niet kunnen testen, omdat de vocalisaties van jongere vogels minder duidelijk te karakteriseren zijn en de analyse ervan vereist dat de huidige methodes eerst verder ontwikkeld worden.

Ik bespreek de algemene inzichten die ik tijdens mijn onderzoek verkregen heb in een breed theoretisch kader en hoewel mijn experimenten onder gecontroleerde omstandigheden plaatsgevonden hebben, is het mogelijk voorzichtige extrapolaties te maken en uitspraken te doen over zebravinken in het algemeen. De experimenten die ik in mijn proefschrift beschrijf hebben waardevolle resultaten opgeleverd, maar sommige vragen blijven open en sommige hypotheses moeten nog getest worden. Daarom geef ik in het laatste hoofdstuk ook enkele suggesties voor vervolgonderzoek.

Franz Marc

Franz Moritz Wilhelm Marc was born in Munich on February 8th 1880 as the second son of painter/artist Wilhelm Marc and his wife Sophie. It took him quite some time to decide on what he wanted to become, but in 1899 he registered as a student at the faculty of philosophy of the Ludwig-Maximilian-Universität in Munich. He planned on starting with his study right after military service. However, during his obligatory time in the army he realised that he would rather become a painter/artist. In autumn 1890 he started a course at the "Münchener Akademie", but quit in 1893. In 1911 he got acquainted to Wassily Kandinsky, with whom he organised two expositions of the "Redaktion des Blauen Reiters" and published the "Almanach der Blaue Reiter".

Franz Marc is most famous for his paintings of animals, like "Blaues Pferd I" (1911) and "Der Tiger" (1912), which were created in a period of only 4 years. The less well known painting "Waldinneres mit Vogel" on the cover of this dissertation also has its origin in this period. In previous years he moved from traditional Munich Academy painting, over various other styles to the development of his own personal "Formensprache" ("language of form").

Franz Marc has been travelling quite a lot and met many interesting people everywhere, but he always returned to Upper Bavaria. In August 1914 he volunteered for the war, as did his friend and colleague August Macke, who got killed in the autumn of the same year. On March 4th 1916 Franz Marc died in a shellfire and his body was brought to Kochel am See in 1917, where it has been buried since. Many of his works are now permanently on display in the Franz Marc Museum in Kochel am See, which was opened in 1986.

Franz Marc – Waldinneres mit Vogel 1912 - Kunstmuseum Bern

Sources:

Marc. Susanna Partsch 2005. Taschen GmbH Köln
Der Blaue Reiter. Hajo Düchting, Norbert Wolf (HG) 2009. Taschen GmbH Köln.

Franz Marc

Franz Moritz Wilhelm Marc wurde am 8. Februar 1880 in München geboren, als zweiter Sohn des Malers Wilhelm Marc und seiner Frau Sophie. Lange war er sich über seinen späteren Werdegang unschlüssig, aber 1899 schrieb er sich als Student an der Philosophischen Fakultät der Ludwig-Maximilian-Universität in München ein. Er hatte vor, direkt nach dem Militärdienst mit dem Studium anzufangen. Während seiner Militärzeit wurde ihm jedoch bewusst, dass er eigentlich Maler werden wollte. Im Herbst 1890 fing er eine Lehre an der Münchener Akademie an, hörte 1893 aber wieder damit auf. 1911 lernte er Wassily Kandinsky kennen, und auf diese Begegnung folgten zwei Ausstellungen der "Redaktion des Blauen Reiters" und die Veröffentlichung des "Almanach der Blaue Reiter".

Franz Marc ist vor allem bekannt und beliebt wegen seinen Tierdarstellungen, wie z.B. "Blaues Pferd I" (1911) und "Der Tiger" (1912), die in einer Periode von knapp vier Jahre entstanden. Das weniger bekannte "Waldinneres mit Vogel" auf der Vorderseite dieser Dissertation stammt ebenfalls aus dieser Periode. Die Jahre zuvor hat Franz Marc gebraucht, um von der traditionellen Malerei der Münchener Akademie über verschiedene Stil-richtungen zu seiner persönlichen "Formen-sprache" zu kommen.

Franz Marc ist relativ viel gereist und hat überall interessante Bekanntschaften gemacht, aber er kehrte immer wieder nach Oberbayern zurück. Im August 1914 meldete er sich als Kriegsfreiwilliger, ebenso wie sein Freund und Kollege August Macke, der im Herbst des gleichen Jahres fiel. Am 4. März 1916 wurde Franz Marc von einem Granatdoppelschuß tödlich getroffen, und 1917 wurde sein Leichnam nach Kochel am See gebracht, wo er seither begraben liegt. Seit 1986 gibt es in Kochel am See das Franz Marc Museum, wo viele seiner Werke permanent ausgestellt werden.

Franz Marc

Franz Moritz Wilhelm Marc werd op 8. Februar 1880 geboren in München, als tweede zoon van schilder Wilhelm Marc en zijn vrouw Sophie. Lange tijd wist hij niet wat hij later wilde worden, maar in 1899 schreef hij zich in bij de filosofische faculteit van de Ludwig-Maximilian-Universität in München. Hij was van plan direct na zijn militaire dienst met de studie te beginnen, maar tijdens zijn diensttijd ontdekte hij dat hij toch liever schilder wilde worden. In de herfst van 1890 begon hij een opleiding aan de Münchener Akademie, waar hij in 1893 weer mee ophield. In 1911 leerde hij Wassily Kandinsky kennen en op deze ontmoeting volgden 2 tentoonstellingen van de "Redaktion des Blauen Reiters" en de publicatie van de "Almanach der Blaue Reiter".

Franz Marc is vooral bekend en geliefd vanwege zijn schilderijen van dieren, zoals bv. "Blaues Pferd I" (1911) en "Der Tiger" (1912) die hij in een periode van krap vier jaar maakte. Het minder bekende werk "Waldinneres mit Vogel" op de voorkant van dit proefschrft stamt ook uit deze periode. De voorafgaande jaren gebruikte Franz Marc om van de traditionele schilderkunst van de Münchener Akademie via verschillende stijlen uiteindelijk zijn persoonlijke "Formensprache" ("vormentaal") te ontwikkelen.

Franz Marc heeft relatief veel gereisd en overal interessante mensen leren kennen, maar hij is altijd weer teruggekeerd naar Oberbayern. In augustus 1914 melde hij zich als vrijwilliger voor de oorlog, net als zijn vriend en collega August Macke, die in de herfst van dat jaar viel. Op 4 maart 1916 werd Franz Marc dodelijk getroffen door een Granatdoppelschuß en in 1917 werd zijn lichaam naar Kochel am See gebracht, waar hij sindsdien begraven ligt. In 1986 werd het Franz Marc Museum in Kochel am See geopend, waar veel van zijn werk permanent tentoongesteld wordt.

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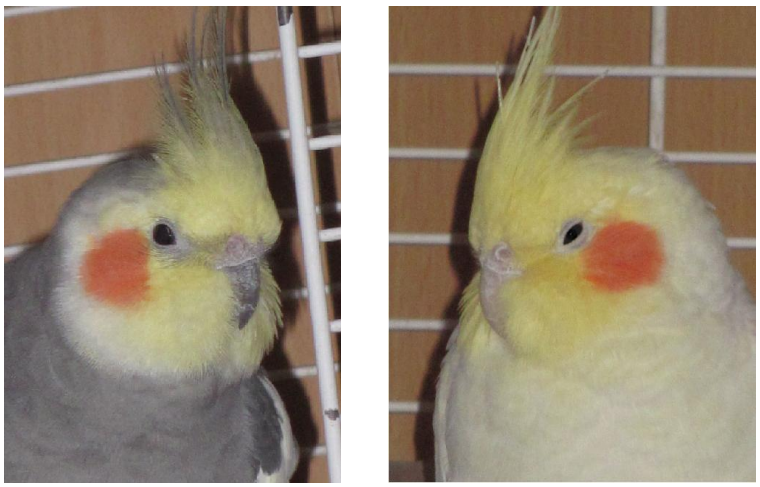

Luna & Helios

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Poot, H.; Ter Maat, A.; Trost, L.; Schwabl, I.; Jansen, R.F. and Gahr, M. 2012. *Behavioural and physiological effects of population density on domesticated Zebra Finches (Taeniopygia guttata) held in aviaries.* Physiology & Behavior 105:821-828

Conference Contributions

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Poster: *Juvenile Zebra Finches and their favourite teachers*

24th International Congress for Conservation Biology, Edmonton, Alberta. 2010.
Oral Presentation: *Bird-Friendly Light?*

Ethological Society Meeting: Cooperation and Conflict, Zurich. 2011.
Poster: *Behavioural and physiological effects of population density on domesticated Zebra Finches (Taeniopygia guttata) in aviaries*

Symposium Université Franco-Allemande/ Deutsch-Französische Hochshule: Animal communication: mechanisms, consequences and social aspects, Paris. 2011.
Oral Presentation: *Song learning in a multi-tutor environment*

Mini-workshop Bats & Light (the effects of artificial lighting on bats in Europe), Sensory Ecology Group, Max-Planck-Institute for Ornithology. 2012.
Oral Presentation: *Green light for nocturnally migrating birds?!*

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Oral Presentation: *Verhalten bei Singvögeln*

Declaration

Eidesstattliche Erklärung

Ich versichere hiermit an Eides statt, dass die vorgelegte Dissertation von mir selbständig und ohne unerlaubte Hilfe angefertigt ist.

München, den ....
(Unterschrift)

Erklärung

Hiermit erkläre ich,

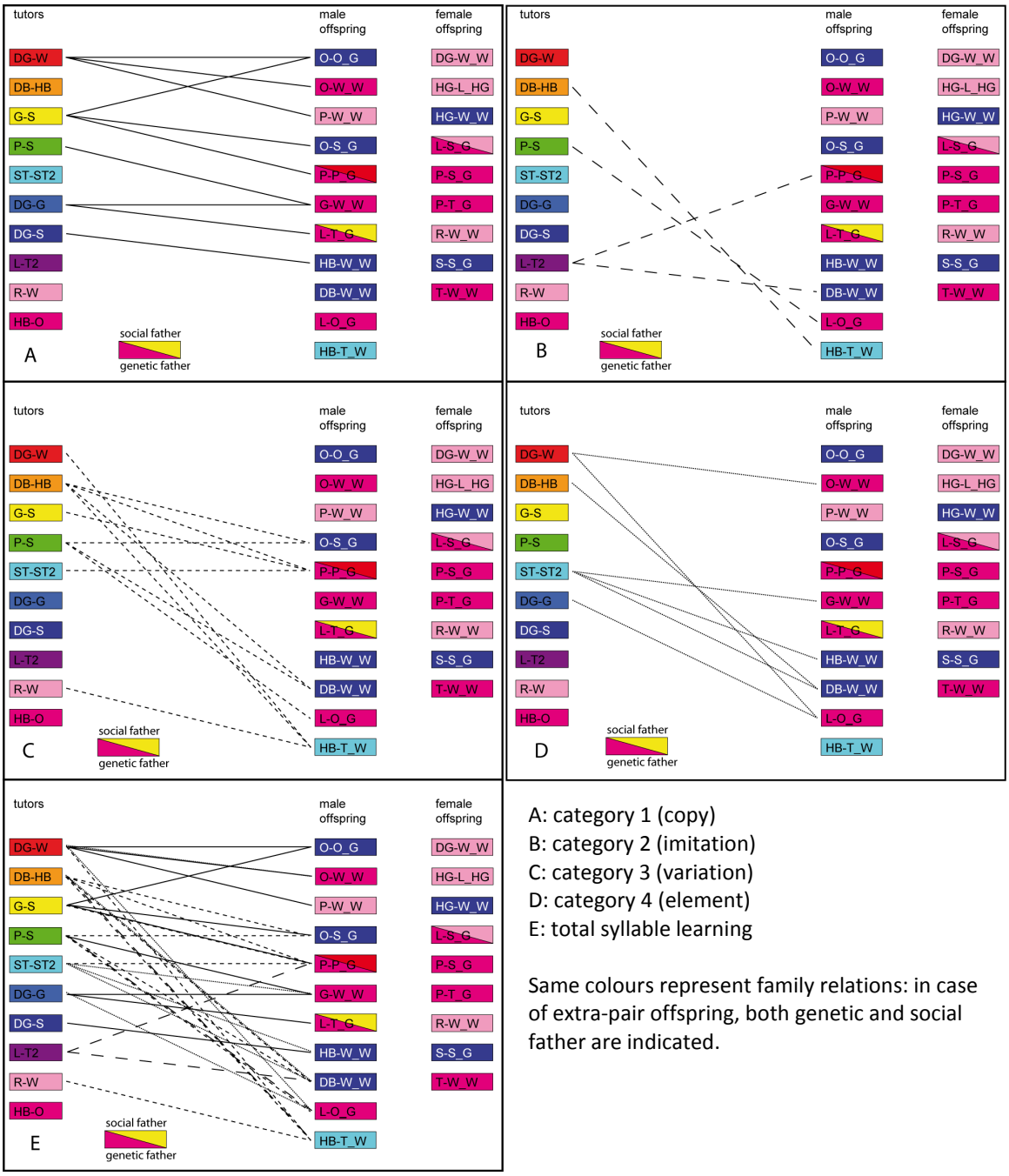
☐ dass die Dissertation nicht ganz oder in wesentlichen Teilen einer anderen Prüfungskommission vorgelegt worden ist.

☐ dass ich mich anderweitig einer Doktorprüfung ohne Erfolg nicht unterzogen habe.

München, den..... .....
(Unterschrift)

Appendix

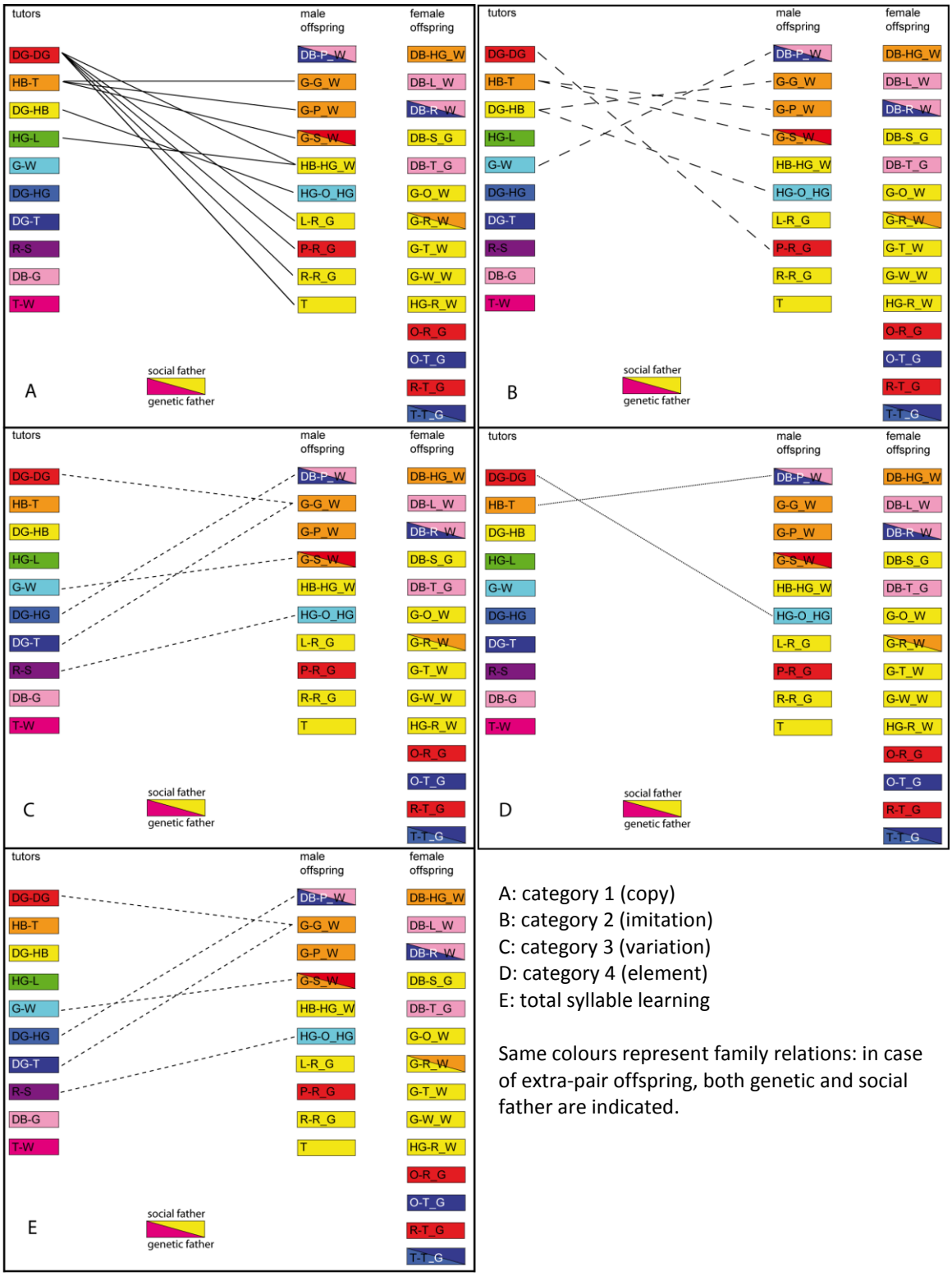
Syllable Learning – Aviary 1



A: category 1 (copy)
B: category 2 (imitation)
C: category 3 (variation)
D: category 4 (element)
E: total syllable learning

Same colours represent family relations: in case of extra-pair offspring, both genetic and social father are indicated.

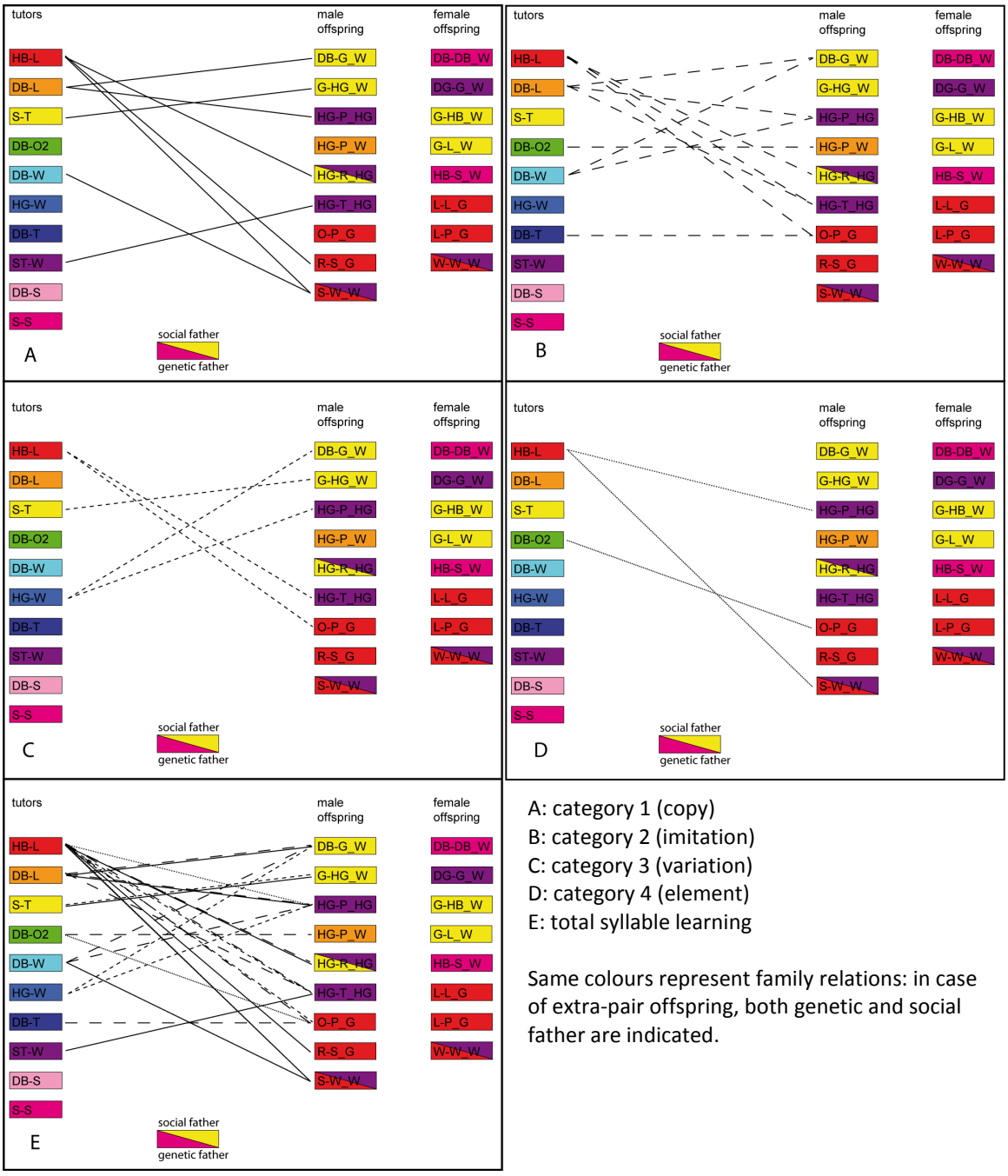
Syllable Learning – Aviary 2



A: category 1 (copy)
B: category 2 (imitation)
C: category 3 (variation)
D: category 4 (element)
E: total syllable learning

Same colours represent family relations: in case of extra-pair offspring, both genetic and social father are indicated.

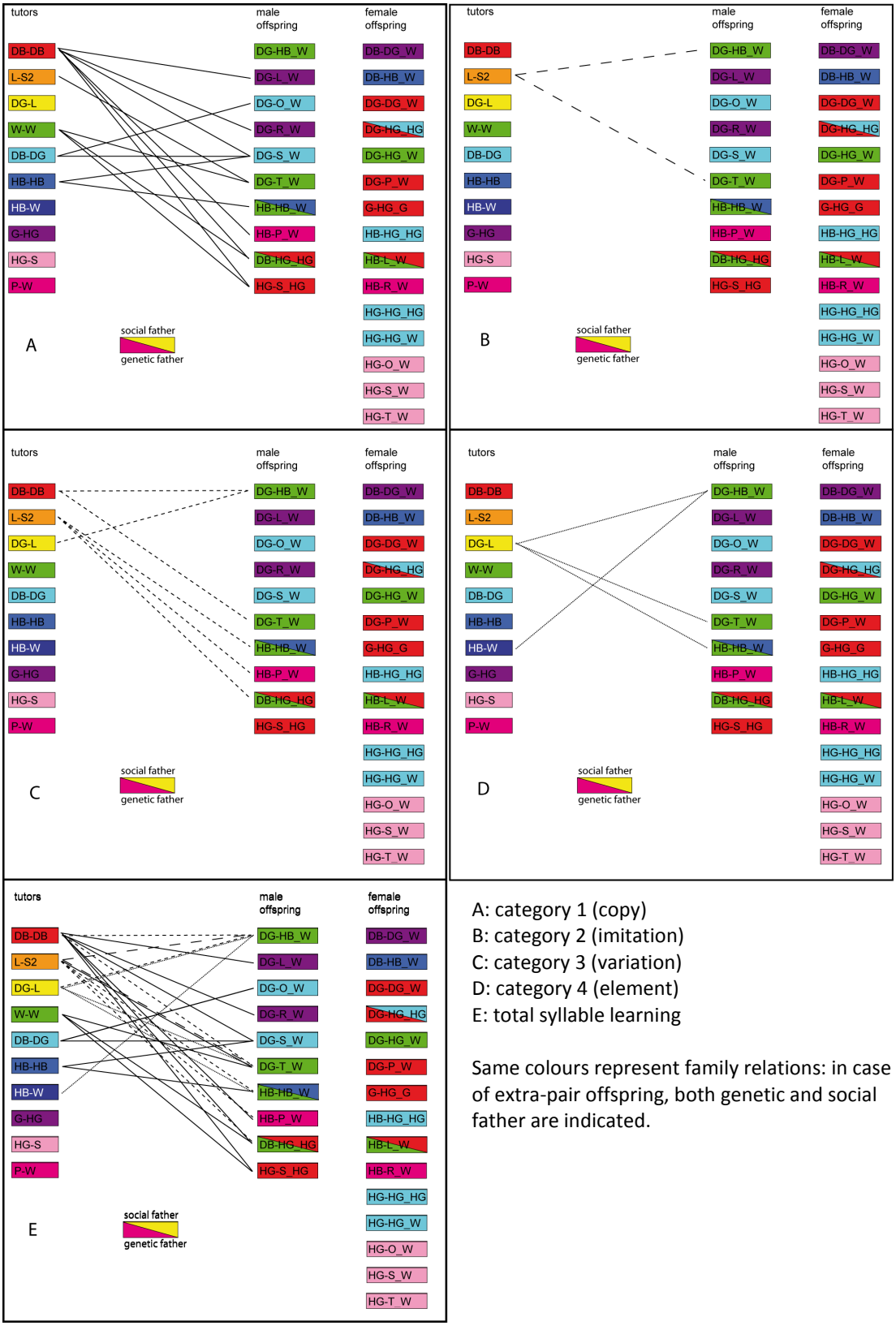
Syllable Learning – Aviary 3



A: category 1 (copy)
B: category 2 (imitation)
C: category 3 (variation)
D: category 4 (element)
E: total syllable learning

Same colours represent family relations: in case of extra-pair offspring, both genetic and social father are indicated.

Syllable Learning – Aviary 4



A: category 1 (copy)
B: category 2 (imitation)
C: category 3 (variation)
D: category 4 (element)
E: total syllable learning

Same colours represent family relations: in case of extra-pair offspring, both genetic and social father are indicated.

Syllable Sharing

Syllable sharing among siblings in aviary 1,3 and 4. Same colours represent family relations: in case of extra-pair offspring, both genetic and social father are indicated.

aviary 1	L-T_G	G-W_W	O-W_W	L-O_G	P-P_G	P-W_W	HB-T_W	HB-W_W	O-O_G	O-S_G	DB-W_W
L-T_G											
G-W_W											
O-W_W						2			1		
L-O_G											
P-P_G									1	1	2
P-W_W			2						4		
HB-T_W											
HB-W_W											1
O-O_G			1		1	4				1	
O-S_G					1				1		1
DB-W_W					2			1		1	

aviary 3	DB-G_W	G-HG_W	HG-R_HG	HG-P_HG	HG-T_HG	S-W_W	O-P_G	R-S_G	HG-P_W
DB-G_W				4					
G-HG_W									
HG-R_HG									
HG-P_HG	4								
HG-T_HG							1		
S-W_W								2	
O-P_G					1				
R-S_G						2			
HG-P_W									

aviary 4	HB-HB_W	DG-HB_W	DG-T_W	DB-HG_HG	HG-S_HG	DG-O_W	DG-S_W	DG-L_W	DG-R_W	HB-P_W
HB-HB_W				2			1			1
DG-HB_W			1							
DG-T_W		1		1	1					
DB-HG_HG	1		1		4			3	3	4
HG-S_HG			1	4			1	3	3	3
DG-O_W							1			
DG-S_W	1				1	1		1	1	1
DG-L_W				3	3		1		6	6
DG-R_W				3	3		1	6		6
HB-P_W	1			4	3		1	6	6	

Data-Tables

Characterisation of all adult males (tutors) in aviary 1, 3 and 4. Percentage of all learned offspring syllables that could be attributed to this tutor; was the male paired to a female (yes/no); total number of offspring that survived at least until day 100 post hatching; number of extra-pair offspring (EPO) from total number of offspring; social rank, based on agonistic interactions, with rank 1 = most dominant male; body mass at begin of experiment in gram. These tables present a synthesis of data from chapter 2-5.

Aviary 1

tutor	learned	paired	offspring	EPO	rank	mass
DB-HB	13.6%	no	0	0	8	16.9
DG-G	6.8%	no	0	0	3	19.9
DG-S	4.5%	yes	8	0	6	18.63
DG-W	31.8%	yes	1	1	7	15.65
G-S	13.6%	yes	1	0	2	22.03
HB-O	0.0%	yes	6	0	4	17.04
P-S	13.6%	no	0	0	10	11.8
T-L	4.5%	yes	1	0	5	14.35
R-W	2.3%	yes	5	1	1	17.51
ST-ST	9.1%	yes	1	0	9	16.85

Aviary 3

tutor	learned	paired	offspring	EPO	rank	mass
DB-O	8.6%	no	0	0	7	17.74
DB-S	0.0%	no	0	0	6	21.27
DB-W	8.6%	yes	1	0	10	19.9
HB-L	37.1%	yes	4	0	2	15.23
HG-W	5.7%	yes	0	0	2	17.54
DB-L	20.0%	yes	3	1	5	17.38
S-S	0.0%	yes	3	0	4	16.59
ST-W	2.9%	yes	3	0	1	17.83
DB-T	2.9%	yes	0	0	8	18.2
S-T	14.3%	yes	5	1	9	13.73

Aviary 4

tutor	learned	paired	offspring	EPO	rank	mass
DB-DB	55.1%	yes	5	0	1	19.77
DB-DG	4.1%	yes	5	0	2	18.76
G-HG	0.0%	yes	3	0	5	21.48
HB-HB	4.1%	yes	1	0	7	21.42
HB-W	2.0%	yes	0	0	4	20.38
HG-S	0.0%	yes	4	0	6	17.5
DG-L	12.2%	no	0	0	10	17.42
L-S	16.3%	no	0	0	9	13.74
P-W	0.0%	yes	2	0	8	14.76
W-W	6.1%	yes	6	3	3	16.27

Leg Ring Colours

DB	dark blue	(DunkelBlau)
DG	dark green	(DunkelGrün)
G	yellow	(Gelb)
HB	light blue	(HellBlau)
HG	light green	(HellGrün)
L	lilac	(Lila)
O	orange	(Orange)
P	pink	(Pink)
R	barbie-pink	(Rosa)
S	black	(Schwarz)
ST	striped	(STreifen)
T	red	(roT)
W	white	(Weiss)